NOTE TO USERS

Duplicate page number(s); text follows.
The manuscript was scanned as received.

pages 107, 136

This reproduction is the best copy available.

UMI®

University of Alberta

Effectiveness of an Artificial Stream in Providing Productive Fish Habitat in the Canadian Arctic

by

Nicholas Edward Jones

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of

Doctor of Philosophy

in

Environmental Biology and Ecology

Department of Biological Sciences

Edmonton, Alberta
Spring 2004

Library and Archives Canada

Published Heritage Branch

395 Wellington Street
Ottawa ON K1A 0N4
Canada

Bibliothèque et Archives Canada

Direction du Patrimoine de l'édition

395, rue Wellington
Ottawa ON K1A 0N4
Canada

Your file Votre référence
ISBN: 0-612-96283-0
Our file Notre référence
ISBN: 0-612-96283-0

The author has granted a non-exclusive license allowing the Library and Archives Canada to reproduce, loan, distribute or sell copies of this thesis in microform, paper or electronic formats.

L'auteur a accordé une licence non exclusive permettant à la Bibliothèque et Archives Canada de reproduire, prêter, distribuer ou vendre des copies de cette thèse sous la forme de microfiche/film, de reproduction sur papier ou sur format électronique.

The author retains ownership of the copyright in this thesis. Neither the thesis nor substantial extracts from it may be printed or otherwise reproduced without the author's permission.

L'auteur conserve la propriété du droit d'auteur qui protège cette thèse. Ni la thèse ni des extraits substantiels de celle-ci ne doivent être imprimés ou aturement reproduits sans son autorisation.

In compliance with the Canadian Privacy Act some supporting forms may have been removed from this thesis.

Conformément à la loi canadienne sur la protection de la vie privée, quelques formulaires secondaires ont été enlevés de cette thèse.

While these forms may be included in the document page count, their removal does not represent any loss of content from the thesis.

Bien que ces formulaires aient inclus dans la pagination, il n'y aura aucun contenu manquant.

Canada

Abstract

Few fish habitat compensation projects are rigorously assessed with respect to the principle of "no net loss" of productive capacity. To examine the effectiveness of a 3.4-km artificial stream in the Northwest Territories, Canada, I used reference streams to understand fish-habitat relationships and diet of YOY (young-of-the-year) Arctic grayling *(Thymallus arcticus*) and to develop standards against functions of the artificial stream (e.g., production fish) could be compared. The artificial stream restored watershed connectivity, allowing fish migration, and provided spawning and nursery habitat, particularly for Arctic grayling. However, the mass of individual YOY grayling at the end of summer was 57% lower in the artificial stream than in natural streams. This difference in growth, in concert with estimates of grayling density, meant that the standing crop produced in the artificial stream averaged 37% of that found in natural streams. A bioenergetics model indicated that cooler water temperatures in the artificial stream had limited influence on growth. However, low amounts of autochthonous and allochthonous organic matter and poor physical habitat in the artificial stream appeared to limit the productivity of benthic invertebrates and fish. Resource selection functions developed for YOY grayling in natural streams indicated that there was an abundance of quality habitat for small grayling in the artificial stream, but a paucity of quality habitat for the larger YOY grayling. Habitat structures created to "enhance" the productive capacity of the artificial stream provided benefits at the local, but not at the whole-stream scale. Annual climatic variability and lake-outlet ecology affected the production of grayling in both the natural and artificial streams. Successful habitat compensation in this artificial stream will not likely be fully realized until more allochthonous and autochthonous organic matter is available to the benthic fauna and fish.

This thesis is dedicated, with appreciation and wonder, to the rivers and lakes of Canada and all their inhabitants

Acknowledgements

I would like to thank my supervisor Bill Tonn and members of my supervisory committee for their guidance and support throughout my thesis. I thank all the hard working field crew members, including Marcina Crosier, Scott Dunbar, Beverly Gingras, Nahum Lee, Giselle Marion, Maria Sotiropoulos, and Scott Stewart. Special thanks to Marek Janowicz for many hours of laboratory work. Family and friends, particularly the cohort of 1998, enriched my graduate school experience with their support and understanding.

This research was made possible through grants and in-kind support from BHP Billiton Diamonds Inc. Additional financial support came from the Canadian Circumpolar Institute (Northern Scientific Training Program and Circumpolar/Boreal Alberta Research), a National Sciences and Engineering Research Council of Canada (NSERC) Industrial Postgraduate Scholarships with BHP Billiton Diamonds Inc, and an NSERC research grant to W.M. Tonn. Alberta Research Council kindly provided equipment. Additional graduate student support included a Walter John's Memorial Fellowships, D. Alan Birdsall Memorial Scholarships, and John & Patricia Schloser Environmental Scholarship.

Table of Contents

CHAPTER I: GENERAL INTRODUCTION 1
Literature Cited 5

CHAPTER II: ECOLOGICAL CHARACTERISTICS OF STREAMS IN THE BARRENLANDS NEAR LAC DE GRAS, N.W.T., CANADA 7
Introduction 7
Study Area 9
Methods 10
Physicochemical characteristics *10*
Biological characteristics *12*
Statistical analyses *13*
Results 14
Physicochemical characteristics *14*
Biological characteristics *16*
Discussion 20
Physicochemical characteristics *20*
Biological characteristics *22*
Variability among years *25*
Tundra streams, lake-outlets, and fish growth *26*
Literature Cited 29

CHAPTER III: SELECTIVE FEEDING OF AGE-0 ARCTIC GRAYLING IN LAKE-OUTLET STREAMS OF THE NORTHWEST TERRITORIES, CANADA 46
Introduction 46
Methods 48
Young-of-the-year habitat use and foraging behaviour *48*
Field sampling *49*
Laboratory analyses *50*
Statistical analyses *50*
Results 52
Composition of drift and diet *52*
Spatiotemporal variation in drift and diet *52*
Prey selection *53*
Discussion 54
Literature Cited 58

CHAPTER IV: PRODUCTIVE CAPACITY OF AN ARTIFICIAL STREAM IN THE CANADIAN ARCTIC: ASSESSING THE EFFECTIVENESS OF COMPENSATION 69
Introduction 69
Study System 71
Methods 73
General sampling design *73*
Basic stream surveys (stream physical characteristics and fish) *73*

Benthic stream surveys (limnology, woody debris, epilithon, CPOM, and benthic invertebrates) *74*
Intensive stream sampling (temperature, drift, fish growth, biomass, and density) *76*
Bioenergetic model and simulations *78*
Statistical analyses *80*
Results 80
Physicochemical *80*
Biological *82*
Bioenergetic simulations *86*
Discussion 87
Assessing the artificial stream as productive fish habitat *87*
Growth of YOY Arctic grayling *88*
Perspective 94
Literature Cited 96

CHAPTER V: RESOURCE SELECTION FUNCTIONS FOR AGE-0 ARCTIC GRAYLING (*THYMALLUS ARCTICUS*) AND THEIR APPLICATION TO STREAM HABITAT COMPENSATION 114
Introduction 114
Methods 116
Habitat availability *118*
Habitat use *118*
Model development *119*
Model validation *120*
Assessment of habitat in the artificial stream *121*
Results 122
Habitat availability and use: Polar-Vulture stream *122*
Model validation *125*
Assessment of habitat in the artificial stream *125*
Discussion 125
Model validation *128*
Assessment of habitat in the artificial stream *130*
Literature Cited 132

CHAPTER VI: ENHANCING PRODUCTIVE CAPACITY IN THE CANADIAN ARCTIC: ASSESSING THE EFFECTIVENESS OF INSTREAM HABITAT STRUCTURES IN HABITAT COMPENSATION 143
Introduction 143
Study System 145
Methods 146
Structure-Scale Assessment *147*
Artificial stream-Scale Assessment *148*
Results 150
Structure-Scale Assessment *151*
Artificial stream-Scale Assessment *152*
Discussion 153
Structure-Scale Assessment *153*
Stream-Scale Assessment *155*

Structure Effectiveness: Scale of Measurement and the Role of Energy *156*
Literature Cited 158

CHAPTER VII: GENERAL DISCUSSION 173
Literature Cited 183

List of Tables

Table 2-1. Physical characteristics of the 20 study streams from the Lac de Gras region of the Barrenlands, N.W.T., Canada that were used in the principal component analysis of Figure 2-2. Fine substrates include clay, silt, and sand, and coarse substrates include cobble and boulder. Group numbers refer to the four groups of streams from Figure 2-2. A single asterisks indicates streams sampled for benthic invertebrates, water chemistry, woody debris, organic matter, and epilithon. A double asterisks indicates streams intensively sampled for fish and drifting invertebrates. 35

Table 2-2. Annual variation (1998-2000) in accumulated mean monthly air temperature and precipitation, and accumulated mean daily degree-days and mean daily discharge from 1 June to September 1, and date of freshet initiation for the study area and streams in the Barrenlands, NWT, in relation to several biotic characteristics of the streams. Numbers in parentheses are standard errors among streams for Polar-Vulture, Pikejaw, and Slipper-Lac de Gras, except for drift density and YOY length and mass, which are from Polar-Vulture. ANOVAs and multiple comparisons were used to determine significant differences among years. 36

Table 2-3. Physical and chemical properties of water from Barrenland streams in late July, 1998-2000. Ranges from Alaskan tundra streams are provided for comparison (see text). SE is standard error among streams and n is the number of streams sampled. 36

Table 2-4. Characteristics of coarse particulate organic matter (CPOM), and biota from study streams in the Barrenlands, NWT. Data are from late-July, 1998-2000, except for fork length and mass of young-of-the-year (YOY) arctic grayling (from late August). CPOM, epilithon, and benthic density and biomass are subdivided into riffles and pools, all of which were significantly different except for benthic densities. SE is standard error and n is the number of streams sampled. Min and max represent the minimum and maximum values from all samples..... 37

Table 2-5. Comparison of mean density and percentage composition of benthic invertebrates and drift. Benthos data are from nine Barrenland streams, 1998-2000, whereas, drift data are from Polar-Vulture stream in 1999 and 2000, and Pigeon Creek in 2000. The composition of Diptera is further subdivided into four groups by percent composition. Invertebrate densities for benthos are shown as individuals m^{-2} and for drift, as individuals $100m^{-3}$..... 38

Table 2-6. Frequency of occurrence (%) of fish species and average fish community composition (%) among 18 Barrenland study streams, NWT, Canada. 40

Table 3-1. Physical characteristics of Polar-Vulture and Pigeon streams, Northwest Territories, Canada..... 62

Table 3-2. Invertebrate taxa identified in the stomachs of YOY Arctic grayling and drift samples collected from Polar-Vulture (1998-2000) and Pigeon (2000) streams.

Invertebrates were classified as large or small based on body size. In 2000, Diptera were divided into Chironomidae, Simuliidae, and Culicidae. For some analyses, Cladocera, Copepoda, and Ostracoda were grouped together (as microcrustacea), as were Ephemeroptera, Plecoptera, and Trichoptera (as ETP). Where possible, insects were identified as larvae, pupae, and adult. 63

Table 4-1. Physiological parameters used in the bioenergetics model for YOY Arctic grayling. 102

Table 4-2. Mean percentage total cover (± standard error) and its distribution among cover types available to young-of-the-year Arctic grayling in the artificial and two natural streams, Polar-Vulture and Pigeon. Significance (p value) indicate differences between the artificial and natural streams (one sample hypothesis testing). Aquatic and terrestrial vegetation were very scarce in the artificial stream. NA, not applicable. 104

Table 4-3. Temperature regime characteristics of the artificial (ART) and natural streams, Polar-Vulture (PV) and Pigeon (PG), from swim-up of young-of-the-year Arctic grayling to 31 August 1998 - 2001. Mean temperature is the overall seasonal average of mean daily temperatures, which are the average of six measurements per day. Mean difference is the difference in mean daily temperatures between natural stream(s) and the artificial stream, averaged over the season. The mean daily temperature in the artificial stream was significantly lower (paired t-tests, $p < 0.05$) in all comparisons with natural streams. Standard errors are in parentheses..... 105

Table 4-4. Annual variation in weather and discharge during June - August, and accumulated degree-days from spawning to 23 August in relation to mean ± standard error epilithon mass, benthic invertebrate density for Polar-Vulture, Pikejaw, and Slipper-Lac de Gras streams, 1998 - 2001. Data on young-of-the-year mean size ± standard error are from Polar-Vulture. For 1998, fish mass on 23 August was estimated based on two prior sampling periods (9 July and 30 July). General linear modelling and multiple comparisons were used to assess differences in biotic characteristics among years. YOY = young-of-the-year. 106

Table 4-5. Mean mass (g) ± standard error and the absolute and relative difference in mass of young-of-the-year Arctic grayling between the artificial and natural streams on 23 August 1998 – 2001, shortly before out-migration. Number of natural streams studied per year are: 1998 (1), 1999(2), 2000 (9), and 2001(3)..... 107

Table 4-6. Results of bioenergetics simulations for 1998 – 2001. Relative influence of temperature and food on young-of-the-year Arctic grayling growth as estimated from the simulations. Natural streams are Polar-Vulture (PV) and Pigeon (PG).. 107

Table 5-2. Dates and sizes of young-of-the-year (YOY) Arctic grayling when habitat use and availability observations were made in the Polar-Vulture (PV) and the artificial stream (ART) in 1999. 137

Table 5-3. Analysis of deviance table showing the statistical significance (P value) and R^2 values of the independent variables in the parametric logistic regression model for small young-of-the-year Arctic grayling in Polar-Vulture, a natural Barrenland stream. % of R^2 is the percentage that each variable contributed to the total coefficient of determination. Italics indicate variables that had significant nonlinear effects. Null model residual deviance was 512 with 727 degrees freedom. 138

Table 5-4. Analysis of deviance table showing the statistical significance (P value) and R^2 values of the independent variables in the parametric logistic regression model for large young-of-the-year Arctic grayling in Polar-Vulture, a natural Barrenland stream. % of R^2 is the percentage that each of the variable contributed to the total coefficient of determination. Italics indicate variables that had significant nonlinear effects. Null model residual deviance was 426 with 547 degrees freedom. 139

Table 6-1. Description of each structure type, the type of habitat type(s) it provides, the function of each structure with respect to the habitat needs of adult and YOY Arctic grayling, and the general influence on water velocities and depths (Wesche, 1985; Lowe, 1989; Rosgen, 1996). 163

Table 6-2. Mean length and area ± standard error of stream electrofished at sections of stream modified with structures and sections of stream used as controls in the artificial stream. 164

List of Figures

Figure 2-1. Map showing the Lac de Gras study area, with study stream locations indicated by black dots (•). Numbers within dots correspond to streams listed in Table 2-1. Insert: location of study area in the Northwest Territories, Canada..... 41

Figure 2-2. Principal components analysis ordination of the 20 study streams (numbered as in Table 1), based on seven physical variables. Vectors (arrows) point in the direction of increasing values for the respective variables, with vector length reflecting the strength 42

of the relationship. Shaded ellipses highlight four groups of physically similar streams (see text for details)..... 42

Figure 2-3. Mean ± SE drift biomass found at Polar-Vulture Creek on 12 July, 15 July, 30July, and 29 August 1999. Estimates for each date are based on 18 samples except for 43

the caribou stream crossing estimate (July 12), which is from a single sample collected 30 min. after a herd of ca. 100 caribou crossed Polar-Vulture. 43

Figure 2-4. Relationship between number of fish species found in 18 study streams and the minimum summer discharge, based on surveys in mid-August, 2000. 44

Figure 2-5. Relationships of mean fork length of YOY Arctic grayling in late August to latitude of individual streams (upper) and growing degree-days (5°C) (lower) in north western Canada (black diamonds) and Barrenland streams (open circle). Error bars are ranges from 10 Barrenland streams during 1998-2000. Comparison data and linear regressions are from the Mackenzie Valley and Yukon North Slope drainages (figure modified from McCart, 1986). Barrenland climate data are from Contwoyto Lake, Northwest Territories (65°29'N 110°22'W) (Environment Canada 1991), adjusted to match McCart (1986), who defined growing degree-days from a base of 4.4°C (40°F). 45

Figure 3-1. Percentage composition of invertebrates in the drift and diet of young-of-the-year Arctic grayling and drift during summers 1998 (upper) and 1999 (lower) in Polar-Vulture Creek. Ephemeroptera, Trichoptera, and Plecoptera, (ETP) were grouped. Number of stomachs examined for diet analyses are given in parentheses. Eighteen drift samples were collected per date..... 64

Figure 3-2. Percentage composition of invertebrates in the diet of young-of-the-year Arctic grayling and drift from Polar-Vulture and Pigeon Creeks in 2000. Number of stomachs examined for diet analyses are given in parentheses. Eighteen drift samples were collected per date..... 65

Figure 3-3. Mean (± 95% confidence interval) dietary preference (Jacob's D) by young-of-the-year Arctic grayling from Polar-Vulture (solid circles) and Pigeon Creeks

(open circles) in 2000. Positive values indicate preference and negative values indicate avoidance. Prey taxa are arranged left to right by decreasing size. Sample size was 120 stomachs per stream (i.e., 4 samples of 30 fish)..... 66

Figure 3-4. Mean (± SE) head capsule widths of larval Chironomidae (upper) and Simuliidae (lower) in the drift (squares) and diet of young-of-the-year Arctic grayling (diamonds) in Polar-Vulture (left) and Pigeon creeks (right), July-August 2000. Significant differences (Mann-Whitney tests, $P < 0.05$; with Bonferroni adjustment) are indicated with an asterisk. Average sample size per date is 22. 67

Figure 3-5. Mean (± SE) percentage composition of different life history stages of Chironomidae (upper) and Simuliidae (lower) in the diet of young-of-the-year Arctic grayling (grey) and drift (black) from Polar-Vulture and Pigeon creeks during July-August, 2000. Significant differences (Mann-Whitney tests, $P < 0.05$; with Bonferroni adjustment) are indicated with an asterisk. Sample sizes for Polar-Vulture are 72 and 120, and for Pigeon are 66 and 123, for drift and stomach samples, respectively. 68

Figure 4-1. Map showing the location of the artificial stream in relation to lakes in the watershed. Koala Lake and the dark portion of Panda Lake were drained and developed as open-pit mines. Water flow, indicated by the arrows, moves from Vulture Lake to Polar Lake through the artificial stream and into Kodiak Lake. Insert: location of study area in the Northwest Territories, Canada. 108

Figure 4-2. Mean (± standard error) amounts of (a) epilithon, and (b) substrate coarse particulate organic matter (CPOM), and benthic invertebrate (c) density and (d) biomass in riffle and pool habitats from the artificial (black) and natural streams (grey), 1998 - 2000. Asterisks indicate significant differences (t-test, $p < 0.05$) between stream types. AFDM = ash-free dry mass. 109

Figure. 4-3. Mean (± standard error) densities in the drift of (a) small (e.g., microcrustaceans) and (b) large (e.g., insects) invertebrates and (c) total drift biomass (dry mass) in the artificial (black) and natural streams, Polar-Vulture (light grey) and Pigeon (dark grey), during four sampling periods 1999 – 2000. Letters indicate significant differences among streams (General linear modeling and multiple comparisons, $p < 0.05$) for each time period; NS = not significant. N = 18 per stream and time period. ND = no data. 110

Figure 4-4. Mean (± standard error) (a) density and (b) biomass of all fish and of (c) grayling in pool and riffle habitats in the artificial (black) and Polar-Vulture (grey) streams in 1998 - 2000. Asterisks indicate significant differences (t tests; $p < 0.05$) between streams. 111

Figure 4-5. The mass of young-of-the-year Arctic grayling (*Thymallus arcticus*) in relation to (a) date and (b) fork length for the artificial (solid circles) and natural streams (open circles). All mass and length data points are means of samples collect during the summers of 1998 - 2001. 112

Figure 4-6. Mean mass (± standard error) of young-of-the-year (YOY) Arctic grayling (*Thymallus arcticus*) on 23 August in relation to the number of degree-days (water temperatures above 0 °C) accumulated by the artificial streams (solid line and circles) and Polar-Vulture (dashed line and open circles) streams between the date of spawning by grayling to 23 August. Masses on 23 August 1998 were estimated for both streams from large samples collected on 9 and 30 July 1998. Also indicated are least-squares regression lines and equations. 113

Figure 5-1. Two views of Polar-Vulture, the natural stream (top), and of the artificial stream (bottom). 140

Figure 5-2. Resource selection curves for small and large young-of-the-year Arctic grayling in a natural Barrenlands stream (Polar-Vulture). Some variables did not significantly (NS) contribute to the models but were still of general interest. Vegetation plot (bottom right-hand corner) represents aquatic (solid black lines) and terrestrial vegetation (solid grey lines). Index of selection is standardized to range from high (1) to low (0) probability of use. 141

Figure 5-3. Predicted probability of use for habitat that was available to (a,c) and used by (b,d) small (a,b) and large (c,d) young-of-the-year Arctic grayling in the artificial stream, based on resource selection functions from the natural Barrenland stream (Polar-Vulture). 142

Figure 6-1. Map showing the location of the artificial stream in relation to lakes in the watershed. Koala Lake and the dark portion of Panda Lake were drained and developed as open-pit mines. Water flow is indicated by the arrows. The locations of fish habitat structures are indicated along the artificial stream. Insert: location of study area in the Northwest Territories, Canada. 165

Figure 6-2. Pictures of the artificial stream (top) and a representative natural stream (bottom) 166

Figure 6-3. Planar views of each structure (a) ramp, (b) v-weir, (c) vanes, and (d) groin constructed in the artificial stream. Arrows indicate general direction of water movement. 167

Figure 6-4. Mean density (a) and mass (b) ± SE of young-of-the-year Arctic grayling in relation to downstream distance from the lake outlet from control sections of the artificial stream in late July 2000. A 900 m stretch of the artificial stream, approximately midway between the source and mouth, is inaccessible to sampling. 168

Figure 6-5. Mean ± SE density and biomass of fish at each structure and associated control sections of stream in late July (a) and August (b), 2000. Asterisks indicate significant differences (t-test with Bonferroni adjustment, $P < 0.05$) 169

Figure 6-6. Mean ± SE mass of young-of-the-year Arctic grayling at each structure and associated control sections of stream in late July 2000. Average sample size is 147

fish per section of stream. Asterisks indicate significant differences (t-test, $P < 0.05$). 170

Figure 6-7. Mean ± SE density (a) and biomass (b) of fish in pool and riffle habitats in the artificial stream (ART) and Polar-Vulture stream (PV) in late-July, 1998 to 2000. Differences between the artificial stream and Polar-Vulture, expressed as percentages of the latter, are is listed above each bar. Dashed lines indicate pre- and post- construction periods for the structures. 171

Figure 6-8. Growth rates ± SE of young-of-the-year Arctic grayling from swim-up to late-August for the artificial stream (ART) and three natural streams 1998-2001. Polar-Vulture (PV), Pigeon (PG), Polar-Panda (PP). Percentage difference between the artificial stream and natural streams are listed for each year along the abscissa. Dashed division lines indicate pre- and post-construction of the structures..... 172

Chapter I: General Introduction

The supply and suitability of habitat ultimately limit fish populations (Minns 1997). In Canada, the principle legislation for the conservation and management of fisheries and fish habitat is the *Fisheries Act*. Under the *Act*, strategies to manage fish habitat focus on preventing the harmful alteration, disruption, or destruction (HADD) of habitats that sustain fish productivity (Minns 1997). In 1986, the Department of Fisheries and Oceans clarified their position regarding the management and protection of fish habitat (Policy for the Management of Fish Habitat, DFO 1986). The intent of this policy was to ensure that management of fish habitat in Canada operated under the guiding principle of "no net loss of productive capacity of fish habitats" (NNL). Productive capacity is defined in the policy as "the maximum natural capability of habitats to produce healthy fish, safe for human consumption, or to support or produce aquatic organisms upon which fish depend." Both HADD and NNL require the ability to quantify the effects habitat change has on productive capacity of an aquatic ecosystem. In turn, this presumes that the habitat needs of the resident species are understood, that the relationship between habitat and fish production are known or can be assessed, and that there is an undisturbed natural area or time prior to disturbance that can serve as a reference point with which to measure the effectiveness of restorative or enhancement measures (Minns 1997). Often, however, one or more of these presumptions are not met.

Freshwater ecosystems of the Arctic and subarctic are among the least studied and most poorly understood in North America (Rouse et al. 1997; Schindler 2001). Evidence

for this can be seen in the paucity of published literature on Arctic grayling (*Thymallus arcticus*), even though it is a key species of the Canadian north for tourism and as a food source in many communities (Scott and Crossman 1973; Northcote 1995). In their reviews, Armstrong (1986) and Northcote (1995) pointed out major gaps in our knowledge of Arctic grayling ecology. For instance, little is known about the role critical habitats play in controlling grayling population size and productivity during key periods in their life history.

Although considerable variation exists from location to location, grayling life history typically involves cyclic migrations among spawning, feeding, and overwintering habitats (Craig and Poulin 1975; Armstrong 1986; Northcote 1995). In the spring, adult grayling migrate from overwintering areas of larger rivers, spring-fed streams, and lakes to small tributaries (Warner 1957), where they spawn over riffles of coarse to fine gravel (Northcote 1995). Larvae of European grayling, *Thymallus thymallus*, first move into quiet backwaters following hatching but, upon reaching a length of ca. 25-35 mm, move into faster water in the vicinity of the natal area and feed on invertebrate drift for the summer (Scott 1985; Sempeski and Gaudin 1995); it is assumed the young-of-the-year (YOY) Arctic grayling use similar nursery areas (Armstrong 1986). Older grayling migrate away from spawning and nursery habitats to different feeding areas, often choosing habitats according to age and sexual maturity (Armstrong 1986), e.g., in some cases, grayling size increases with decreasing stream order (Hughes and Reynolds 1994). In the fall, all grayling migrate back to overwintering areas (Armstrong 1986).

Exploitation of natural resources continues to expand into the Canadian north. In 1991, diamonds were discovered in the remote Barrenlands region near Lac de Gras in

the Northwest Territories (300 km northeast of Yellowknife). In preparation for mineral extraction, two lakes and their tributary streams were drained. As part of a Habitat Compensation Agreement between BHP-Billiton Diamonds Inc. and the Department of Fisheries and Oceans, BHP-B designed and constructed a 3.4 km "diversion channel" and associated structures to enhance fish habitat. Water is now diverted around Panda and Koala Lakes through a constructed stream, the Panda Diversion Channel (often referred to here as the artificial stream). Construction of the stream was completed in 1997 and fish-habitat structures were added in the fall of 1998. It was anticipated that the artificial stream would restore watershed connectivity, allowing fish migration, primarily Arctic grayling, while habitat structures would provide spawning and nursery habitats, again for grayling, improving the artificial stream's productive capacity for grayling.

Despite widespread use of stream habitat enhancement and restoration elsewhere (see White 1996), there has been little research into the effectiveness of such programs in a northern environment. Although the addition of habitat structures a year after the stream was constructed permits a before/after investigation of the effects of those specific structures, natural streams were also used to examine the artificial stream as a whole. As presumed under HADD and NNL (Minns 1997), understanding the habitat requirements of Arctic grayling is needed to effectively protect, restore, or create habitats that are threatened or affected by development, and to assess measures taken to achieve those objectives. In particular, there is little information about the effects of habitat modification on grayling distribution, habitat use, and production (Armstrong 1986: Hunter and Fernet 1990), or even on the relationships between habitat productivity, food supply, and grayling production in Barrenland streams (Armstrong 1986; Northcote

1995). These relationships are critical for predicting, understanding, and assessing the effects of habitat modification and enhancement (Hayes et al. 1996; Minns 1997).

The principal objective of my thesis is to evaluate the effectiveness of the artificial stream, and the added habitat structures, in providing productive fish habitat. To answer this, I address a set of smaller, more specific, objectives.

1. Describe the ecological characteristics of natural streams in the Barrenlands near Lac de Gras, Northwest Territories, Canada.
2. Examine the selective feeding of YOY Arctic grayling in lake-outlet streams of the Northwest Territories, Canada.
3. Assess the productive capacity of the artificial stream and thus, the effectiveness of fish habitat compensation program.
4. Develop resource selection functions for YOY arctic grayling in a natural Barrenlands stream and use them to assess the quality of physical habitat in the artificial stream.
5. Evaluate the effectiveness of specific habitat structures added to the artificial stream.

Addressing each of the five objectives will contribute new information on the ecology of Barrenland streams and Arctic grayling that, when integrated (General discussion and conclusions, Chapter VII), will provide a synthesis on the initial effectiveness of the artificial stream to compensate for lost fish habitat and demonstrate an approach to the design and evaluation of habitat compensation programs.

Literature Cited

Armstrong, R.H. 1986. A review of Arctic grayling studies in Alaska, 1952-1982. Biological Papers of the University of Alaska. No. 23.

Craig, P.C. and Poulin, V. 1975. Movements and growth of Arctic grayling (*Thymallus arcticus*) and juvenile Arctic char (*Salvelinus alpinus*) in a small arctic stream, Alaska. J. Fish. Res. Bd. Can. 32: 689-697.

Department of Fisheries and Oceans (DFO). 1986. The Department of Fisheries and Oceans policy for the management of fish habitat. Communications Directorate, Fisheries and Oceans, Ottawa, Ontario.

Hayes, D.B., Ferreri, C.P., and Taylor, W.W. 1996. Linking fish habitat to their population dynamics. Can. J. Fish. Aquat. Sci. 53(Suppl. 1): 383-390.

Hughes, N.F., and Reynolds, J.B. 1994. Why do Arctic grayling (*Thymallus arcticus*) get bigger as you go upstream? Can. J. Fish. Aquat. Sci. 51: 2154-2163.

Hunter, C.J. and Fernet, D. 1990. Enhancement of Arctic grayling spawning in Hyalite Creek, Montana and the development of spawning habitat utilization curves. Proc. Ann. Conf. West. Assoc. Fish Wildl. Agen.70

Minns, C.K. 1997. Quantifying "no net loss" of productivity of fish habitats. Can. J. Fish. Sci. 54: 2463-2473.

Northcote, T.G. 1995. Comparative biology and management of Arctic and European grayling (Salmonidae, Thymallus). Rev. Fish Bio. Fish. 5: 141-194.

Rouse, W.R., Douglas, M.S.V., Hecky, R.E., Hershey, A.E., Kling, G.W., Lesack, L., Marsh, P., McDonald, M., Nicholson, B.J., Roulet, N.T. and Smol, J.P. 1997. Effects

of climate change on the freshwaters of Arctic and subarctic North America. Hydrological Processes 11: 873-902.

Schindler, D. W. 2001. The cumulative effects of climate warming and other human stresses on Canadian freshwaters in the new millennium. Can. J. Fish. Aquat. Sci. 58: 18-29.

Scott, A. 1985. Distribution, growth, and feeding of post-emergent grayling *Thymallus thymallus* in an English River. Trans. Amer. Fish. Soc. 114: 525-531.

Scott, W.B., and Crossman, E.J. 1973. Freshwater fishes of Canada. Bulletin 184. Fisheries Research Board of Canada, Ottawa. Pages 300-305.

Sempeski, P., and Gaudin, P. 1995. Size-related changes in diel distribution of young grayling (*Thymallus thymallus*). Can. J. Fish. Aquat. Sci. 52: 1842-1848.

Warner, G.W. 1957. Environmental studies on grayling as related to spawning, migration and distribution. U.S. Fish and Wildlife Service and Alaska Game Commission. Federal Aid in Fish Restoration, Quarterly Progress Report. Project F-1-R-7, Work Plan C, Job 3b, 7(3). 14 pp.

White, R.J. 1996. Growth and development of North American stream habitat management for fish. Can. J. Fish. Aquat. Sci. 53(Suppl. 1): 342-363.

Chapter II: Ecological Characteristics of Streams in the Barrenlands near Lac de Gras, N.W.T., Canada

Introduction

In the last 50 years, arctic regions have experienced a steady expansion in the development of their natural resources. With this growth, there has been an increase in local environmental pressures and impacts, while regionally, the Arctic is being affected by depletion of ozone, climate warming, and long-distance transport of contaminants (Schindler 2001). These increased pressures have not been matched by increases in research directed toward assessing, predicting, or mitigating ecosystem impacts, or even defining reference conditions needed to take such actions (Reist 1997).

For the reference-condition approach of impact assessment to succeed, data on physical, chemical, and biological conditions from an appropriate set of minimally impacted reference sites are required to compare against potentially impaired sites (Reece et al. 2001). In many areas of North America, development has left few "pristine" ecosystems available for use as reference sites (e.g., Benke 1990). This severely limits our ability to make sound management decisions or to evaluate the success of those decisions, despite our increasing knowledge of many ecosystems (Minns 1996; Karr and Chu 1999). In the Arctic, however, the problem is nearly the reverse (Oswood, 1997); there are many ecosystems still in relatively pristine condition, yet we know little about their ecological characteristics. For effective protection, management, and restoration of arctic

ecosystems, more knowledge is needed concerning the characteristics of appropriate, reference sites.

This lack of information applies to the physical, chemical, and biological characteristics of arctic streams and rivers (Schindler 2001), although there are exceptions, notably from Alaska. Pioneering studies (e.g., Watson et al. 1966; Kalff 1968) surveyed large areas, tending to collect physicochemical data, but made few comparisons within a broader context. More synthetic was Craig and McCart's (1975) classification of stream types in Beaufort Sea drainages, based mainly on physiographic characteristics. In 1983, the R4D program (Response, Resistance and Resilience to, and Recovery from, Disturbances in Arctic Ecosystems) was established, focusing efforts on the Imnavait Creek watershed in the Northern Foothills of the Brooks Range, Alaska (e.g., Everett et al. 1989; Kane et al. 1989; Oswood et al. 1989; Oswood 1989; Miller and Stout 1989; Irons and Oswood 1992). Since 1978, research on the Kuparuk River, Alaska, has provided valuable insight into biological and chemical processes of arctic rivers (Peterson et al. 1993; Hershey et al. 1997). More recently, Kling et al. (2000) investigated the spatial and temporal patterns of change in limnological variables of streams in the Toolik Lake District. In addition, a large body of gray literature has been generated in response to resource development; however, most have focused on specific, local concerns and are rarely placed in a larger context, (e.g., to establish regional reference conditions).

In the present study, I examine the physical, chemical, and biological characteristics of streams in the Barrenlands region of the Northwest Territories, Canada. Specifically, I ask: what is the pattern of variation in the physical characteristics of Barrenland streams?

Are these patterns reflected in chemical and biological characteristics? How does annual variability in climate and the physicochemical characteristics of streams stream affect stream biota? My intention is to use these observations to establish reference conditions for the region. To enhance our general understanding of low arctic rivers and streams, I also make comparisons of the largely lake-outlet Barrenland streams with other arctic stream ecosystems.

Study Area

The 4000 km^2 study area is centred around 64°45'N and 110°30'W (see Fig. 2-1), about 100 km north of the tree-line within the southern arctic ecozone. The physiographic region is the Kazan Upland and is underlain by granite, gneiss, and schist that form broad, sloping uplands, plateaus, and lowlands. Eskers, kames, and boulder-strewn till plains cover the land. The mean annual temperature is approximately -12°C, with a summer maximum of 27.2°C and a winter minimum of –53.9°C (Environment Canada, 1991). The climate is semi-arid with 200–300 mm precipitation annually, 50% of which falls as snow. The permafrost layer is continuous. Thin soils in upland areas support dwarf-heath and scattered low-shrub tundra, while lowland and depressional areas near lakes and streams are characterized by sedge tussock and low-tall shrub tundra (Bliss 1981).

The combination of relatively low topographical relief (ca. 50 m) and extensive glacial activity has molded a landscape covered by ca. 21% water in the form of numerous chains of lakes and connecting streams. Following spring runoff, evaporation from lakes gradually lowers lake level, stream flows diminish, and surface flow is lost

from many small streams. At approximately 450 meters above sea level, the streams of this area are the headwaters of the Coppermine, Back, and Burnside Rivers, which flow north to the Arctic Ocean.

Methods

Data were collected during three summers, 1998-2000, from streams representing a range of physical characteristics observed in the Barrenlands region. Stream selection was mainly based on proximity to base camp (within a ca. 40 km radius) and the presence of visible water in the stream channel during initial surveys in late July. Initially nine core streams were sampled for benthic invertebrates, water chemistry, woody debris, substrate coarse particulate organic matter, epilithon, basic physical characteristics, and fish community composition. Two of these streams, Polar-Vulture and Pigeon, were subjected to intensive fisheries and invertebrate drift investigations. In 2000, an additional eleven streams were surveyed for basic physical characteristics and fish community composition.

Physicochemical characteristics

Stream geomorphology, including length, drainage area, slope, bankfull width and depth, and substrate composition, were determined on the ground and from aerial photographs, and topographic maps for the twenty streams. Stream length was measured as the thalweg distance from the upstream lake to the downstream lake. Substrate composition was quantified along several transects perpendicular to stream flow and classified as clay and silt (<0.0625 mm), sand (0.0625 – 2 mm), small gravel (2 – 32 mm), large gravel (32 – 64 mm), cobble (64 – 256 mm), and boulder (>256 mm). Discharge measurements

were made manually once for each stream in late-July to mid-August, with additional data collected by automated stage recorders.

Weather data were collected during the ice-free season from a meteorological station situated in a central location on the study area. On a daily basis, rain was measured with an automatic tipping bucket. Air temperature (± 0.5°C) was measured automatically every hour at a height of 1.9 m above ground level. HOBO Temp loggers recorded stream water temperature (± 0.1°C) in Polar-Vulture and Pigeon streams every four hours.

For the nine core streams limnological variables were measured in the field. Dissolved oxygen concentrations (± 0.01 mg/L) were determined with a WTW Multiline P4 portable meter fitted with a CellOx 325 probe. Conductivity (±1 µS/cm) and pH (±0.01 pH unit) were measured with the same meter fitted with a TetraCon 325 and SenTix 41 probe, respectively. Turbidity (± 0.1 nephelometric turbidity units) was measured using a Global Water turbidity meter. Stream water samples for later laboratory analysis were stored in a cold, light-free environment. All samples were collected in late July. Three samples were collected from each stream.

In the laboratory, total nitrogen was analysed using the persulfate digestion method and determined on a Technicon Autoanalyzer. Total organic carbon (TOC) in 1999 and dissolved organic carbon (DOC) in 2000 were determined using a Shimadzu total organic carbon analyzer Model (TOC –5000A) fitted with an ASI – 5000A autosampler. DOC samples were filtered (0.5 µm) prior to measurement. Total phosphorus (± 1 µg/L) was determined spectroscopically using persulfate–oxidized samples by molybdate blue

absorption. Total suspended solids were determined gravimetrically from total residue retained by a standard glass fibre filter (0.45 μm), dried to a constant weight at 105 °C.

Biological characteristics

All woody debris longer than 10 cm were counted along 40 to 150 m lengths of stream channels for the nine streams. The mean diameter of wood pieces was determined by averaging the diameters at each end, whereas the length of each piece was the distance between the two ends. These measurements were then used to calculate volume estimates. Woody debris volume was standardized (as $cm^3/100m^2$) by multiplying the transect length by the mean stream width measured at four locations along the transect.

Five replicate samples of substrate coarse particulate organic matter (CPOM), epilithon, and benthic invertebrates were collected from the nine core streams in late-July in both riffles (mean depth and velocity, 0.24 m and 0.25 m/s; n = 9) and pools (mean depth and velocity, 0.34 m and 0.08 m/s; n = 8). CPOM samples were from substrate cores, 90 mm deep by 80 mm diameter. Within 48 hours, samples were washed, removing inorganic material and invertebrate cases and exuviae, and sieved through 1 mm mesh. Filtered organics on the screen were dried to constant mass at 40°C (± 0.1 mg). Epilithon samples were scraped from the upper surfaces (4.9 or 9.6 cm^2) of randomly selected stones. Invertebrates visible without the aid of magnification were removed from scrapings. Samples were stored frozen in the dark for 2 to 4 weeks before being dried at 40°C, weighed, ashed at 550°C, and reweighed for ash-free dry mass determination (± 0.1 mg). Benthic invertebrate samples were collected using a 0.093 m^2 (one sq. ft.) Surber sampler with 0.25 mm mesh. All samples were preserved with 70%

ethanol in the field. Invertebrates were identified to genus or species, with the exception of Nematoda, Turbellaria and terrestrial invertebrates, which were typically identified to Family or Order. Following enumeration, samples were dried to constant mass at 40°C (± 0.1 mg).

Invertebrate drift was sampled in July-August from Polar-Vulture in 1999 and from Polar-vulture and Pigeon streams in 2000 with two Field-Dodgson tri-net drift samplers (0.25 mm mesh). Samples were collected three times in the summer 1999 and four times in 2000. During each period, samples were collected at dawn, noon, and dusk. Drift samples were preserved in 70% ethanol and later counted and identified as described for benthos.

Eighteen streams were electrofished at least once over the course of the study to determine fish community composition and catch-per-unit-effort (fish per minute). To assess their first summer growth, I collected of young-of-the-year arctic grayling (*Thymallus arcticus*) from one, two, and ten streams in late summer, just before the out-migration, in 1998, 1999, and 2000, respectively. For both types of sampling, captured fish were identified, enumerated, weighed (± 0.01 g) and measured (fork length ±1 mm).

Statistical analyses

I applied principal component analysis, using the correlation matrix, to summarize the pattern of variation among all 20 streams based on seven physical characteristics (see Table 2-1). I used analysis of variance (ANOVA) to compare chemical and biological variables among the resulting groups of streams. Linear regression was used to examine relationships of chemical and biological variables to the physical characteristics. Logistic

regression was used to examine the presence of pike in relation to physical characteristics. ANOVAs were also used to examine among-year variability in biotic characteristics; significant ANOVAs were followed by Tukey multiple comparison tests. Lastly, paired t-tests were used to determine if densities or biomass of coarse particulate organic matter, epilithon, and benthic invertebrates differed between riffle and pools. I used the Kolmogorov-Smirnov test to examine data for normality and Levene median test for homogeneity of variances. For all statistical tests, I used a = 0.05 as a critical level of significance (after performing the Bonferroni adjustment, as required to reduce experimentwise error rate).

Results

Physicochemical characteristics

Although physical characteristics varied among the 20 study streams, virtually all Barrenland streams are lake-outlet systems of moderate length (Fig. 2-1, Table 2-1). Streams flow over folded rock and glacial features, creating highly irregular drainage patterns, but occasionally follow trellis and dendritic configurations for short distances. They typically have a low sinuosity, are "braided" (or more appropriately multi-channelled), with up to seven channels, and are dominated (> 50%) by large boulders. Stream channel slope range from 0.1 to 8.9 %, but most were < 3%.

Principal component analysis organized the 20 streams into four groups based on seven physical characteristics (Fig. 2-2, Table 2-1). Axes one and two explained 67 and 27% of the total variance, respectively. Drainage area was not included in the analysis because it was highly correlated with bankfull width (r = 0.55). Group I: these four

streams are short, wide, and boulder dominated. They generally follow weak hydraulic gradients through unconfined channels. Although these streams are moderately deep, their depth-to-width ratios are low. Group II: these seven medium-length streams contain a moderate diversity of substrate sizes, with water flowing through unconfined braided channels of moderate widths with moderate-to-high gradients. Group III: another large group (six streams), it comprises some of the longest and narrowest streams of the region that generally follow one or two confined channels. This group also has the greatest depth-to-width ratios, with some sections of stream being deeper than they are wide. The streams in this group have low-to-moderate stream gradients and a moderate-to-high proportion of fine substrates. Group IV: the three streams in this group are braided, short, and narrow, of moderate gradients and depth-to-width ratios, and contain a mixture of substrate sizes.

Hydrothermal Regime

Climate governs surface hydrological processes of this area. Streams are frozen solid from approximately late-September to late-May; the snow pack melts rapidly during freshet, creating a large peak in discharge. Based on stream hydrographs from Polar-Vulture Creek (BHP Billiton Diamonds Inc., unpublished data), seasonal variation in mean daily discharge is moderately high, ranging from 15 to 100-fold minimum summer flows. Over the summer, water levels fall slowly, substantially reducing flows to side channels or leaving them hydraulically isolated, especially in highly braided streams. In autumn, precipitation increases stream discharges to ca. 5 times minimum summer flows, reconnecting stream channels. Though not measured, groundwater movement is probably limited in this region due to a shallow active layer, relatively low relief, and mud/clay

soils that typically have a low hydraulic conductivity.

General weather conditions varied among the three study years: 1998 was relatively dry and hot, 1999 was moderately wet and cool, and 2000 intermediate. Correspondingly, the initiation date of freshet varied by 17 days among years (Table 2-2). Mean daily discharge also varied by a factor of four among years, being lowest in 1998 and highest in 1999 (Table 2-2). Stream water temperatures often reached 21°C, but daily averages typically ranged between 12-15°C during the summer. Diel fluctuations in temperature averaged 3°C and rarely exceeded 6°C. From June 1 to Sept 1, streams accumulated 960-1226 degree-days above 5°C; I estimate that from ice-out to ice-on, streams would have accumulated an additional 100-200 degree-days.

Water Chemistry

Barrenlands stream water is circumneutral and low in total phosphorus and total nitrogen (Table 2-3). Turbidity, DOC, and suspended solids levels are highest in the spring and fall, coinciding with higher flows. Overall, water chemistry varied little among the core streams (Table 2-3). Only pH varied among the four groups of streams ($F_{3,5} = 36.6$, $P = 0.002$, group I > II > III = IV) and was positively correlated with bankfull width ($r = 0.94$, $n = 9$, $P < 0.001$). There was also a positive correlation between TOC and drainage area ($r = 0.72$, $n = 5$, $P = 0.032$).

Biological characteristics

Organic Matter

Many streams pass through thick growths of dwarf birch and willow, producing considerable quantities of coarse particulate organic matter (CPOM, Table 2-4) and

relatively small pieces of woody debris (mean length and diameter: 370 mm and 5 mm, respectively). Woody debris volumes were 917 ± 350 $cm^3/100m^2$ of stream (mean ± SE). Barrenland caribou (*Rangifer tarandus)* also add sizeable amounts of woody debris when migrating across the streams by trampling the riparian shrubs and kicking pieces into the stream (N. Jones, per. obs.).

The quantity of epilithon ($F_{3,5}$ = 0.05, P = 0.832) and woody debris ($F_{3,5}$ = 1.94, P = 0.222) did not differ among the four groups of streams. There were no correlations between individual physical stream characteristics and epilithon and woody debris. CPOM, however, differed among stream groups ($F_{3,5}$ = 8.43, P = 0.034, group II > III, I = IV). CPOM was also correlated with substrate type, increasing as the percentage of coarse (r = 0.77, P = 0.016) and fine (r = 0.72, P = 0.028) substrates increased. Pools generally contained larger amounts of CPOM (paired t = 2.7, P = 0.015) and epilithon (paired t = 4.1, P = 0.001) than did riffles (Table 2-4). By mid-July, most pools contain an abundance of aquatic plants (e.g., bur-reed, *Sparganium hyperboreum* and mare's-tail, *Hippuris vulgaris*). Riffles contain few instream plants, aside from filamentous algae (*Zygnema* spp.), which would grow profusely in some areas, covering up to 30% of the streambed by mid-August.

Benthic Invertebrates

Dipterans were well represented in all streams, contributing about 43% of all individuals and consisting of 10 families. Chironomidae were numerically dominant (Table 2-5) and comprised 29 genera. Similarly, most benthic biomass (42%) was contributed by Dipterans, 19% of which were chironomids. Dominant members of the poorly represented Ephemeroptera, Trichoptera, Plecoptera (ETP) group included *Baetis*

tricaudatus, Brachycentrus spp., and *Nemoura* spp. Mean density and biomass of benthic invertebrates varied considerably among years (Table 2-2) and streams (Table 2-4), density did not differ among the four groups of streams ($F_{3,5} = 4.52$, $P = 0.087$). Density did however, increase with bankfull depth ($r = 0.84$, $P = 0.005$). Although riffles and pools differed in their organic matter content (CPOM, epilithon), they contained similar numbers of invertebrates (paired $t = 1.4$, $p = 0.170$, Table 2-4).

Invertebrate Drift

Drift was composed mainly of microcrustaceans, including cladocerans, copepods, and ostracods (Table 2-5). The remaining organisms consisted primarily of dipterans, and mites. Drift density differed little between the two streams sampled in 2000 (Table 2-4), but varied greatly between years in Polar-Vulture (Table 2-2). Catastrophic drift was associated with the seasonal caribou migration. For example, on 12 July 1999, a drift sample was collected 50 m downstream from where ca. 100 caribou had crossed the Polar-Vulture stream 30 minutes earlier. This sample contained eight times the drift biomass of a sample measured three days later (Fig. 2-3). Most of the difference was due to larger non-microcrustaceans: the July 12 sample contained 50 times as many as the July 15 sample. The microcrustacean fraction, in contrast, was similar in the two samples.

Fish

Nine species of fish were found in the study streams (Table 2-6). All streams contained at least one species (max. = 6), but modal richness was only three species, typically arctic grayling, burbot (*Lota lota*), and slimy sculpin (*Cottus cognatus*). Arctic grayling were numerically dominant in most streams (Table 2-6). Species richness was strongly and positively related to minimum summer discharge ($r = 0.88$, $P = 0.001$, Fig. 2-4), as well

as basin area ($r = 0.72$, $P = 0.001$), and negatively to the distance to source populations ($r = 0.41$, $p = 0.08$), e.g., the Coppermine River. The presence of pike was marginally related to the difficulty of colonizing a stream, determined by the stream's slope (rise:run), i.e., its elevation above and distance from source pike populations ($r = 0.45$, $p = 0.075$). Catch-per-unit-effort (CPUE) of all fish did not differ among the four stream groups ($F_{3,5} = 1.11$, $P = 0.377$) nor was total CPUE related to any single physical variable.

Adult grayling began their spawning migration from lakes as soon as water began to flow in stream channels. The peak of migration coincided with decreasing discharge after the main freshet, when water temperatures hovered around 0°C. Adult migration was followed by migrations of juvenile grayling and, where they occurred, lake trout and burbot. Once in the streams, male grayling quickly established and defended territories. Spawning activity peaked when water temperatures reached 5°C and was concentrated in moderately fast-flowing, turbulent, and gravelly areas. Fish activity, including migration, aggressive behavior, spawning, and feeding, generally increased over the course of a day as water temperatures increased. After spawning, adult grayling normally spent several days feeding, particularly in large pools, before returning to lakes. Occasionally, adult grayling would be found trapped in pools due to low summer water levels.

Arctic grayling fry were first observed 21 to 24 days (183-192 degree-days) after spawning. At this time, young were 11 to 13 mm in length and yolk sacs were often visible. Young remained in their natal stream, although some were found inhabiting the margins of lakes in August. During the low flows in August, YOY grayling concentrated in the larger pools, some of which became hydraulically isolated from the main stem.

However, by mid-August, the combination of rains and cooler temperatures replenished lakes and streams, increasing discharges and reconnecting channels. At this time, YOY began migrating to the lakes to over-winter. YOY averaged 68.4 mm ± 4.8 SE in fork length (3.0 g ± 0.5 SE), but this varied among years, related to differences in temperature, discharge, and invertebrate densities (Table 2-2).

Although there was considerable variation in the size of YOY grayling among streams (Table 2-4), grayling from the four groups of streams, identified by their physical characteristics, did not differ systematically in this respect ($F_{3,4} = 0.13$,$P = 0.879$), nor did they differ in terms of catch-per-unit-effort of YOY grayling ($F_{3,13} = 1.56$, $P = 0.399$), or % grayling in the fish community ($F_{3,13} = 0.11$, $P = 0.955$). Similarly, individual physical variables did not correlate with ($P > 0.05$) YOY mass in late August, nor with % grayling within the fish community. However, CPUE for YOY grayling, in streams containing grayling, was positively correlated with stream width ($r = 0.64$, $P = 0.020$).

Discussion

Physicochemical characteristics

Although virtually all Barrenland streams originate as lake outlets, and thus share some important attributes (see below), my analyses indicate that they have diverse physical characteristics, including length, width, and substrate composition. Because of covariation among stream attributes, however, I could identify four groups of streams of similar physical characteristics. For example, streams that drained areas of fine sediment tended to have a greater depth-to-width ratios and single, well-defined channels, whereas the boulder-filled streams were typically braided or, more accurately, multi-channelled.

In contrast to the streams typically described as "braided," Barrenland streams have very stable banks, low sediment loads, and discharges that are not highly variable. Sections of land between channels, the islands, are the result of mainly colluvial, not alluvial, processes. Channel degradation in many of the streams has armored the beds with cobbles and boulders, and this material is, by and large, not embedded.

Streams of the Barrenlands appear to share hydrothermal characteristics with streams in arctic Alaska, related to climatic similarities in the two regions (see Oswood et al. 1989; Milner et al. 1997). In both, flows peak rapidly for several days as snow and ice melts (late May), then, stream discharge attenuates slowly as the active layer thaws. By early August, flows can be very low, ceasing altogether in some 1st order streams (Craig and McCart 1975). Precipitation in late August again increases water levels. Although daily averages are 10-14°C in both regions (Craig and McCart 1975; Oswood et al. 1989; Irons and Oswood 1992), tundra streams in Alaska accumulate approximately 1000 degree-days in total (Irons and Oswood 1992), whereas Barrenland streams achieve 1000 degree-days by September 1, with still roughly a month (100-200 degree-days) of ice-free time before freeze-up.

Despite the occurrence of recognizable stream groups based on physical characteristic, I found little evidence of differences in water chemistry among the groups, likely due to the influence of lakes on stream chemistry (Kling et al. 2000). Nevertheless, both pH and TOC increased with stream size, likely reflecting an overall lower position in the catchment basin and the downslope processing of materials (Kling et al. 2000). The location within a stream (upstream vs. downstream) and the characteristics of the upstream lake may have more bearing on water chemistry than the physical and

biological characteristics of the stream itself.

Barrenland streams contain even lower concentrations of nutrients and major ions than Alaskan tundra streams (Table 2-3). Differences in water chemistry between Alaskan and Barrenland sites are likely related to geology, including the abundance of sedimentary versus igneous rock, respectively. Because of extensive permafrost and a thin active layer, however, atmospheric inputs (wet and dryfall) likely supply the majority of the ions to streams within both regions (Everett et al. 1989).

Biological characteristics

Organic matter

Quantities of CPOM in Barrenland streams are relatively high even though the region produces small amounts of leaf litter. High biomass likely reflects low rates of decomposition resulting from an arctic climate and a higher percentage of coarse substrate that fosters retention of CPOM. Unlike Naiman et al. (1987), I did not find that CPOM decreased with stream order or size, likely because the numerous lakes on the Barrenland landscape capture downward moving coarse organics, and thus, interrupt the stream processing of materials (Ward and Standford 1983) or possibly because I did not capture enough variability in stream size.

In contrast to CPOM, catchments in the Barrenlands are similarly vegetated to those in Alaska and supply similar quantities of dissolved and total organic carbon (Peterson et al., 1986; Oswood et al., 1989; Hershey et al., 1997; Table 2-2).

Benthic invertebrates

The composition of the benthic community in Barrenland streams was typical of tundra

streams and rivers in Alaska (Oswood 1989). Generally, the arctic invertebrate fauna is depauperate, and some groups (Odonata and Megaloptera) are usually absent (Miller et al. 1986). Instead, stream invertebrate communities are generally dominated by a diverse group of dipterans, particularly Chironomidae, which can be as species-rich as in temperate streams (Oswood 1989).

Despite their compositional similarity, I found substantially (20-fold) higher densities of benthic invertebrates in Barrenland streams than that found in Alaska. For example, Craig and McCart (1975) found benthic densities ranging from 126 - 2469 ind./m^2 (mean 1025) from 18 streams using a mesh of 9 threads/cm. Miller et al. (1986) reported average densities of 372 to 2128 ind./m^2 in Imnavait Creek using a 363 µm mesh, while Miller and Stout (1989) estimated benthic invertebrate density in Imnavait Creek at 334 - 917 ind./m^2. In contrast, the lowest value I obtained, 1620 ind./m^2, was at the higher end of those recorded from tundra streams in Alaska, and during the warm, dry year of 1998, densities averaged > 31,000 ind./m^2. It seems unlikely that my smaller mesh size (250 µm) accounts for differences in densities between Barrenland and Alaskan streams. Patterns of benthic invertebrate biomass closely followed those of my density estimates in Barrenland streams.

Benthic invertebrate densities were positively correlated to bankfull depth among Barrenland streams. Bankfull depth was generally greater in larger streams, which also tend to carry more flow. These streams, (e.g., Norm's Camp, Ursula, and Slipper-Lac de Gras) are also less likely to freeze solid during the winter, or at least freeze for a shorter period, and thus invertebrates may find refuge and survive. Large streams also likely

moderate spring floods and heavy precipitation events, and thus provide more environmental stability relative to smaller streams.

Invertebrate Drift

Relatively few studies have documented invertebrate drift in the Arctic, and most of this research was done in Alaska (e.g., Miller et al. 1986; Miller and Stout 1989), where *Baetis* mayflies are often the dominant drifter (Hinterleitner-Anderson et al. 1992). In the lake-outlet streams of the Barrenlands, however, zooplankton dominate the drift, producing densities 40-150 times as high as those from Alaskan streams. Even without the microcrustacean component, drift densities were still 2-15 times as high as those recorded for Alaskan streams. If drift density is related to benthic density, as suggested by Miller and Stout (1989), then these differences in non-microcrustacean drift density support my findings of higher benthic invertebrate densities in Barrenland streams than in streams of arctic Alaska.

Exceptionally high drift densities (16,607 ind./100m^3), of which 75% were Diptera, Ephemeroptera, Trichoptera, and Plecoptera, were observed just after Polar-Vulture stream was crossed by a small herd of caribou (ca. 100 individuals). This represents an unusual example of catastrophic drift, elicited by a biotic factor, as opposed to more typical abiotic forces such as spates, pesticides, and acid pulses. Given the nature of the Barrenlands landscape, and the twice-per-year migration of the Bathurst caribou herd, however, it seems likely that this phenomenon is no more unusual for many Barrenland streams than seasonal spates are in other landscapes.

Fish

In comparison to temperate streams, which can have 15-101 species of fish in a stream

(e.g., Horwitz 1978), the streams of the Barrenlands contain few species. A combination of biogeographic and life history constraints creates this impoverished condition (Power 1997). Although stream size (minimum summer discharge and drainage area) was a good predictor of species richness on a regional scale, the occurrence of some uncommon species, e.g., northern pike, depended more on proximity to colonization sources. Interestingly, pike-bearing streams also contained an abundance of mare's-tail while streams without pike did not. These pike streams also had very low grayling abundance, suggesting that these species do not coexist well.

Many streams serve as spawning, nursery, and juvenile habitat for arctic grayling. Adult grayling, lake trout, and round whitefish use small streams primarily in the spring when flows are sufficient for fish passage, but are occasionally found trapped in pools below barriers such as waterfalls, rapids, and boulders. Some may also have been inadvertently swept downstream below barriers at this time, where they subsequently become trapped. By mid-summer, most stream sections contain primarily YOY grayling, along with slimy sculpin and burbot. Some of these YOY grayling can also became trapped in side channels as water levels decline during the summer. The combination of increased precipitation and cooler temperatures in the arctic fall, therefore, might be critical for many populations, allowing fish to migrate back to main branches or lakes before freeze-up.

Variability among years

Invertebrate drift and benthic invertebrate density and biomass varied considerably among the three study years in relation with air and water temperature, rainfall, and

discharge. Correspondingly, YOY grayling were larger in the warm dry year (1998) when food (i.e., invertebrates) was plentiful. Conversely, epilithon abundance was low, perhaps because of high invertebrate numbers. The opposite pattern was observed in the cool wet year (1999). This pattern is consistent with recently observed relationships among growth of YOY grayling, discharge, and water temperature in Alaska (Deegan et al. 1999), suggesting climatic trade-offs; during warm-dry years, fish may experience good growth but also an increased risk of being trapped in an isolated side channel.

Tundra streams, lake-outlets, and fish growth

Craig and McCart (1975) classified streams of the Beaufort Sea drainage into three categories (mountain, spring, and tundra streams) based on their physical, chemical, and biological properties. The general characteristics of their tundra streams were intermediate of spring and mountain streams. With a few exceptions, this description applies to Barrenland streams and perhaps to tundra streams in general.

Nevertheless, there are important differences between tundra streams of Alaska and the Barrenlands, derived ultimately from differences in physical geography. With the exception of the portions of the coastal plain, the Alaskan tundra generally has few lakes, as a consequence, the majority of Alaskan arctic streams are long (30-65 km), continuous, single channelled, and sinuous, many of which in the foothills region are called "beaded" streams (Oswood et al., 1989). Conversely, my study area lies on the Canadian Shield in a landscape that consists of numerous chains of lakes with outlet streams that follow highly irregular drainage patterns over a multitude of glacial features.

The presence of lakes in the Barrenlands modifies the physical, chemical, and

especially biological characteristics of the outlet streams, consistent with the serial discontinuity concept (Ward and Stanford 1983; see also Richardson and Mackay 1991; Kling et al. 2000). Diel temperature fluctuations in Barrenland streams were small (~3 °C) relative to the considerable amplitude (11.6 °C) noted in Alaska (Craig and McCart 1975; Irons and Oswood 1992). Similarly, lakes, can stabilize stream discharge and provide water flow throughout the summer. Drift in Barrenland streams was dominated (90%) by planktonic microcrustaceans of lake origin, compared with *Baetis* in Alaska (Hinterleitner-Anderson et al. 1992). The presence of lakes also concentrates migrating caribou, causing minor stream bank erosion, adding woody debris to the stream, and provoking catastrophic drift. Finally, because of the tight lake-stream relationship, grayling in the Barrenlands exhibit an adfluvial life history (Northcote 1978), residing mainly in the lakes and ascending streams primarily to spawn. This makes their migratory sequence fairly simple compared to the mainly fluvial arctic grayling in Alaska, which make distinct and complex spawning, feeding, and over-wintering migrations (Craig and Poulin 1975).

Such differences in the characteristics of Alaskan and Barrenlands tundra streams appear to propagate to higher trophic levels, ultimately increasing the capacity of the streams to support fish production. To illustrate, the growth of YOY grayling in streams of northwestern North America varies greatly in relation to latitude and climate (growing degree days) (McCart 1986; Fig 2-5). Arctic grayling in Barrenland streams, however, achieve first-year growth rates that are well above the level predicted from McCart's climatic gradient. Because of its more central, continental location, the Barrenland climate is actually comparable to the Yukon's North Slope (Environment Canada 1991),

well to the north, yet YOY grayling grow to a size comparable to that expected from a region with three times the growing degree-days. Because climate generally has a strong influence on the growth of fish (Conover and Present 1990), the discrepancy between observed and predicted growth suggests that specific abiotic and biotic characteristics of Barrenland streams allow YOY to attain larger sizes.

Nutrient levels do not resolve the discrepancy, as Barrenland streams contain some of the most nutrient-poor waters of North America, considerably less than Alaskan and Yukon streams (Watson et al. 1966; Craig and McCart 1975; Oswood et al. 1989; Peterson et al. 1992; and Hershey et al. 1997). Rather, the most striking difference is the lake-outlet nature of Barrenland streams. The characteristics and properties of lake outlets may promote higher productivity than would be observed in continuous streams (see Haraldstad et al. 1987; Hillbricht-Ilkowska 1999; Hieber et al. 2002). Outlet stream temperatures, determined largely by the source lake's epilimnion, are is often warmer and less variable than continuous streams. For arctic grayling on the tundra, higher temperatures inevitability mean longer periods near their thermal optima, resulting in higher growth rates. Most important, perhaps, is the addition of lake-derived energy sources, including the high quality/quantity of seston upon which filter-feeding lotic insects depend (Richardson and Mackay 1991). Although this lake-outlet effect generally attenuates within a few hundred meters (McCreadie and Robertson 1998), most Barrenland streams are relatively short, therefore, influences of the upstream lake should remain significant throughout most of their length. Each of these factors likely contributes to Barrenland outlet streams supporting higher benthic densities and higher rates of grayling growth and production than those found in climatically similar streams

in Alaska and the Yukon. Given that impacts of industrial development on aquatic ecosystems are largely determined in Canada on the basis of effects on their productive capacity for fish (e.g., Minns 1996), it is vital that reference conditions for Barrenlands are understood so that we can account for these differences.

Literature Cited

Benke, A. C., 1990. A perspective on America's vanishing streams. J. North Amer. Benthol. Soc. 9: 77-88.

Bliss, L. C., 1981. North American and Scandinavian tundras and polar deserts. In: Bliss, L.C., Heal, O. W, and Moore, J. J. eds. Tundra ecosystems: a comparative analysis. Cambridge University Press. 8-46.

Conover, D. O. and Present, T. M., 1990. Counter-gradient variation in growth rate: compensation for length of growing season among Atlantic silversides from different latitudes. Oecologia 83: 316-324.

Craig, P. C. and McCart, P. J., 1975. Classification of stream types in Beaufort Sea drainages between Prudhoe Bay, Alaska, and the Mackenzie Delta, N.W.T., Canada. Arctic and Alpine Research 7: 183-198.

Craig, P. C. and Poulin, V. A., 1975. Movements and growth of arctic grayling (Thymallus arcticus) and juvenile arctic char (*Salvelinus alpinus*) in a small arctic stream, Alaska. J. Fish. Res. Board Can. 32: 689-697.

Deegan, L. A., Golden, H. E., Harvey, C. J., and Peterson, B. J., 1999. Influence of environmental variability on the growth of age-0 and adult arctic grayling. Trans. Amer. Fish. Soc. 128: 1163-1175.

Environment Canada, 1991. Canadian climate normals 1961-1990. Ottawa. http://www.msc-smc.ec.gc.ca/climate/climate_normals/index_e.cfm

Everett, K. R., Marion, G. M., and Kane, D. L., 1989. Seasonal geochemistry of an arctic tundra drainage basin. Holarctic Ecology 12: 262-269.

Haraldstad, O., Jonsson, B., Sandlund, O. T., and Schei, T. A., 1987. Lake effect on stream living brown trout (Salmo trutta). Archiv Fur Hydrobiologie 109: 39-48.

Hershey, A. E., Bowden, W. B., Deegan, L. A., Hobbie, J. E., Peterson, B. J., Kipphut, G. W., Kling, G. W., Lock, M. A., Merritt, R. W., Miller, M. C., Vestal, J. R., and Schuldt, J. A., 1997. The Kuparuk River: a long-term study of biological and chemical processes in an arctic river. In: A. M. Milner and M. W. Oswood eds. Freshwaters of Alaska: ecological synthesis. Ecological Studies Series Vol. 119, Springer, Berlin Heidelberg New York. 107-130.

Hieber, M., Robinson, C.T., Uehlinger, U., and Ward, J.V., 2002. Are alpine lake outlets less harsh than other alpine streams? Archiv Fur Hydrobiologie 154: 199-223.

Hillbricht-ilkowska, A., 1999. Shallow lakes in lowland river systems: role in transport and transformations of nutrients and in biological diversity. Hydrobiologia 408/409: 349-358.

Hinterleitner-anderson, D., Hershey, A. E., and Schuldt, J. A., 1992. The effects of river fertilization on mayfly (Baetis spp.) drift patterns and population density in an arctic river. Hydrobiologia 240: 247-258.

Horwitz, R. J., 1978. Temporal variability patterns and the distributional patterns of stream fishes. Ecological Monographs 48: 307-321.

Irons, J. G. III and Oswood, M. W. 1992. Seasonal temperature patterns in an arctic and

two subarctic Alaskan (USA) headwater streams. Hydrobiologia 237: 147-157.

Kalff, J., 1968. Some physical and chemical characteristics of arctic fresh waters in Alaska and Northwestern Canada. J. Fish. Research Board Can. 25: 2575-2587.

Kane, D. L., Hinzman, L. D., Benson, C. S., and Everett, K. R., 1989. Hydrology of Imnavait Creek, an arctic watershed. Holarctic Ecology 12: 279-289.

Karr, J. R and Chu, E. W., 1999. Restoring Life in Running Waters: Better Biological Monitoring. Island Press. Covelo, CA. 220 pages.

Kling, G. W., Kipphut, G. W., Miller, M. M., and O'Brien, W. J., 2000. Integration of lakes and streams in a landscape perspective: the importance of material processing on spatial patterns and temporal coherence. Freshwater Biology 43: 477-497.

McCart, P. J., 1986. Fish and fisheries of the Mackenzie system. In: Davies, B.R. and Walker, K.F. eds. The Ecology of River Systems. Dr. W. Junk Publishers, Boston. 493-515.

McCreadie, J. and Robertson, M., 1998. Size of the larval black fly Simulium truncatum (Diptera: Simuliidae) in relation to distance from a lake outlet. J. Freshwater Ecol. 13: 21-27.

Miller, M. C., Stout, J. R., and Alexander, V., 1986. Effects of a controlled under-ice oil spill on invertebrates of an arctic and subarctic stream. Environmental Pollution (Series A) 42: 99-132.

Miller, M. C. and Stout, J. R., 1989. Variability of macroinvertebrate community composition in an arctic and subarctic stream. Hydrobiologia 172:1,11-127.

Milner, A. M., Irons, J. G., III and Oswood, M. W., 1997. The Alaskan landscape: an introduction for limnologists. In: Milner, A. M., and Oswood, M. W. eds. Freshwaters

of Alaska: ecological synthesis. Ecological Studies Series Vol. 119, Springer, Berlin Heidelberg New York. 1-44.

Minns, C. K., 1996. Detecting the response of fish habitat alterations in freshwater ecosystems. Can. J. Fish. Aquat. Sci. 53 (Supplement 1): 403-414.

Naiman, R. J., Melillo, J. M., Lock, M. A., Ford, T. E., and Reice. S. R., 1987. Longitudinal patterns of ecosystem processes and community structure in a subarctic river continuum. Ecology 68: 1139-1156.

Northcote, T. G., 1978. Migratory strategies and production in freshwater fishes. In: Gerking, S.D., ed. Ecology of Freshwater Fish Production. Oxford: Blackwell, 326-359.

Oswood, M. W., 1997. Streams and rivers of Alaska: a high latitude perspective on running waters. In: Milner, A. M. and Oswood, M. W., eds. Freshwaters of Alaska: ecological synthesis. Ecological Studies Series Vol. 119, Springer, Berlin Heidelberg New York. 331-356.

Oswood, M. W., 1989. Community structure of benthic invertebrates in interior Alaskan (USA) streams and rivers. Hydrobiologia 172: 97-110.

Oswood, M. W., Everett, K. R., and Schell, D. M., 1989. Some physical and chemical characteristics of an arctic beaded stream. Holarctic Ecology 12: 290-295.

Peterson, B. J., Hobbie, J. E., and Corliss, T. L., 1986. Carbon flow in a tundra stream ecosystem. Can. J. Fish. Aquat. Sci. 43: 1259-1270.

Peterson, B. J., Corliss, T., Kriet, K., and Hobbie, J. E., 1992. Nitrogen and phosphorus concentration and export for an Alaskan tundra stream watershed. Hydrobiologia 240: 61-70.

Peterson, B. J., Deegan, L., Helfrich, J., Hobbie, J. E., Hullar, M., Moller, B., Ford, T. E., Hershey, A., Hiltner, A., Kipphut, G., Lock, M. A., Fiebig, D. M., McKinley, V., Miller, M. C., Vestal, J. R., Ventullo, R., and Volk. G., 1993. Biological responses of a tundra river to fertilization. Ecology 74: 653-672.

Power, G., 1997. A review of fish ecology in arctic North America. In: Reynolds, J. ed. Fish ecology in arctic North America. American Fisheries Society Symposium 19, Bethesda, Maryland, USA. 13-39.

Reece, P. F., Reynoldson, T. B., Richardson, J. S., and Rosenberg, D. M., 2001. Implications of seasonal variation for biomonitoring with predictive models in the Fraser River catchment, British Columbia. Can. J. Fish. Aquat. Sci. 58: 1411-1418.

Reist, J. D., 1997. The Canadian perspective on issues in arctic fisheries management and research. In: Reynolds, J., ed. Fish ecology in arctic North America. American Fisheries Society Symposium 19, Bethesda, Maryland. 4-12

Richardson, J. S. and MacKay, R. J., 1991. Lake outlets and the distribution of filter feeders: an assessment of hypotheses. Oikos 62: 370-380.

Schindler, D. W., 2001. The cumulative effects of climate warming and other human stresses on Canadian freshwaters in the new millennium. Can. J. Fish. Aquat. Sci. 58: 18-29.

Ward, J. V. and Standford, J. A., 1983. The serial discontinuity concept of lotic ecosystems. In: Fontaine, T. D. and Bartell, S. M., eds. Dynamics of lotic ecosystems. Ann Arbor Science, Ann Arbor, Michigan. 29-42.

Watson, D. G., Hanson, W.C., Davis, J. J., and Cushing, C. E., 1966. Limnology of tundra ponds and Ogotoruk Creek. In: Wilimovsky, N. J. and Wolfe, J. N., eds.

Environment of the Cape Thompson Region, Alaska. U.S. Atomic Energy Commission. PNE-481: 415-435.

Table 2-1. Physical characteristics of the 20 study streams from the Lac de Gras region of the Barrenlands, N.W.T., Canada that were used in the principal component analysis of Figure 2-2. Fine substrates include clay, silt, and sand, and coarse substrates include cobble and boulder. Group numbers refer to the four groups of streams from Figure 2-2. A single asterisks indicates streams sampled for benthic invertebrates, water chemistry, woody debris, organic matter, and epilithon. A double asterisks indicates streams intensively sampled for fish and drifting invertebrates.

No.	Group	Stream	Drainage area (km^2)	Length (m)	% Slope	Bankfull width (m)	Bankfull depth (m)	Depth:Width	% Fine	% Coarse
1*	I	Norm's Camp	223	600	2.0	35.0	0.89	0.025	5	73
2	I	Nema Martine	114	120	0.2	41.1	0.49	0.012	0	95
3	I	Kodiak-Little	36	80	0.1	43.6	0.50	0.011	0	95
4	I	Moose Nero	87	90	0.1	48.3	0.50	0.010	0	100
5	II	Bedrock	46	520	2.5	14.9	0.49	0.033	10	75
6	II	Sandy	55	350	2.9	9.0	0.45	0.050	8	78
7	II	Nanuq	14	425	0.9	14.7	0.31	0.021	5	75
8*	II	Slipper Rene	176	410	1.2	17.5	0.39	0.022	2	93
9*	II	Slipper Lac de Gras	185	280	2.9	20.0	0.29	0.015	5	80
10*	II	Ursula	86	250	8.0	15.5	0.47	0.031	4	85
11	II	Snow	87	225	8.9	6.2	0.42	0.067	0	95
12	III	Willow	29	2020	1.5	5.1	0.73	0.143	75	20
13**	III	Pigeon	9	2900	0.5	2.4	0.46	0.192	30	58
14*	III	Counts	4	1200	0.6	3.7	0.31	0.083	48	33
15**	III	Polar-Vulture	7	700	1.4	2.7	0.44	0.163	20	55
16*	III	Pikejaw	39	1710	1.8	3.9	0.52	0.135	10	76
17	III	Christine	15	2050	1.2	4.9	0.50	0.102	5	85
18*	IV	Grizzly	7	180	0.4	2.9	0.25	0.087	18	67
19	IV	Polar Panda	9	230	3.0	3.5	0.43	0.123	10	75
20	IV	Cujo	2	150	1.7	2.8	0.21	0.077	20	70
		Median		380	1.5	7.6	0.45	0.058	6	76
		SD		810	2.4	15.1	0.15	0.057	19	20

Table 2-2. Annual variation (1998-2000) in accumulated mean monthly air temperature and precipitation, and accumulated mean daily degree-days and mean daily discharge from 1 June to September 1, and date of freshet initiation for the study area and streams in the Barrenlands, NWT, in relation to several biotic characteristics of the streams. Numbers in parentheses are standard errors among streams for Polar-Vulture, Pikejaw, and Slipper-Lac de Gras, except for drift density and YOY length and mass, which are from Polar-Vulture. ANOVAs and multiple comparisons were used to determine significant differences among years.

Variable	1998 A	1999 B	2000 C	P value & post hoc testing
Air temperature (°C)	37	28	34	
Rainfall (mm)	88	180	118	
Degree-days (°C)	1226	930	1079	
Discharge ($m^3 \cdot s^{-1}$)	2.9	12.8	11.8	
Initiation of freshet	May 14	May 31	May 24	
Epilithon (mg cm^{-2})	1.7 (0.7)	2.0 (0.6)	1.9 (0.4)	0.941
Benthic density (ind. $\cdot m^{-2}$)	31 484 (7541)	3423 (565)	13 720 (1891)	0.046 A B AB
Benthic biomass ($g \cdot m^{-2}$)	13.7 (4.7)	0.5 (0.1)	1.2 (0.3)	0.023 A B B
Drift density (ind. $\cdot 100m^{-3}$)	-	4400 (3235)	14 425 (5686)	0.225
YOY length (mm)	77	56.7 (0.5)	63.9 (0.9)	<0.01 A B C
YOY mass (g)	3.8	1.78 (0.05)	2.55 (0.12)	<0.01 A B C

Table 2-3. Physical and chemical properties of water from Barrenland streams in late July, 1998-2000. Ranges from Alaskan tundra streams are provided for comparison (see text). SE is standard error among streams and n is the number of streams sampled.

Variable	Mean	SE	n	Min - Max	Alaska[a]
DO ($mg\ L^{-1}$)	9.8	0.2	9	8.2-12.0	9.9-12.6
% Saturation	95.3	2.8	9	81.0-121.9	75-100
Conductivity ($\mu S \cdot cm^{-1}$)	14.3	1.1	9	8.0-19.2	21-125
pH	6.78	0.14	9	5.87-7.52	5.3-8.2
Turbidity (NTU)	0.4	0.04	8	0.2-0.5	0.9-1.8
Total suspended solids ($mg \cdot L^{-1}$)	1.78	0.28	8	1.5-3.7	5.4-6.1
Total phosphorus ($\mu g \cdot L^{-1}$)	6.92	0.72	9	4.00-10.20	<10-21
Total nitrogen ($\mu g \cdot L^{-1}$)	167.2	8.9	9	143.3-202.1	~300
Dissolved organic carbon ($mg \cdot L^{-1}$)	3.06	0.12	5	2.56-3.48	2.3-9.6
Total organic carbon ($mg \cdot L^{-1}$)	5.25	0.19	6	4.67-5.83	6.8-9.9

[a] data from Watson et al. (1966), Craig and McCart (1975), Oswood et al. (1989), Peterson et al. (1992), and Hershey et al. (1997).

Table 2-4. Characteristics of coarse particulate organic matter (CPOM), and biota from study streams in the Barrenlands, NWT. Data are from late-July, 1998-2000, except for fork length and mass of young-of-the-year (YOY) arctic grayling (from late August). CPOM, epilithon, and benthic density and biomass are subdivided into riffles and pools, all of which were significantly different except for benthic densities. SE is standard error and n is the number of streams sampled. Min and max represent the minimum and maximum values from all samples.

Variable		Mean	SE	n	Min - Max
CPOM ($g \cdot m^{-2}$)	Riffles	72.2	10.8	9	9.5 – 148.5
	Pools	92.3	7.4	8	15.3 – 218.8
Epilithon ($mg \cdot cm^{-2}$)	Riffles	1.7	0.4	9	0.64 – 4.2
	Pools	2.8	0.4	8	0.9 – 7.26
Benthic biomass ($g \cdot m^{-2}$)	Riffles	9.2	3.7	9	0.26 - 28.9
	Pools	5.2	1.9	8	0.25 – 18.3
Benthic density ($ind. \cdot m^{-2}$)	Riffles	24 037	6139	9	1620 – 90 380
	Pools	15 934	3236	8	2483 – 41 477
Drift density ($ind. \cdot 100m^{-3}$)		12 055	2642	2	152 – 188 690
Drift biomass ($mg \cdot 100m^{-3}$)		156.9	42.4	2	10.9 – 936.7
YOY length (mm)		68.4	4.8	10	42 – 89
YOY mass (g)		3.0	0.5	10	0.78 – 6.29

Table 2-5. Comparison of mean density and percentage composition of benthic invertebrates and drift. Benthos data are from nine Barrenland streams, 1998-2000, whereas, drift data are from Polar-Vulture stream in 1999 and 2000, and Pigeon Creek in 2000. The composition of Diptera is further subdivided into four groups by percent composition. Invertebrate densities for benthos are shown as individuals m^{-2} and for drift, as individuals $100m^{-3}$.

Benthic group	Benthos	Drift
Density (± SE)	23485 (5557)	11999 (2642)
Composition (%)		
Crustacea	11.8	90.4
Diptera	43.2	6.7
(Other Diptera)	*(2.0)*	*(5.5)*
(Chironomidae)	*(84.1)*	*(34.7)*
(Simuliidae)	*(13.9)*	*(57.5)*
(Culicidae)	*(0.0)*	*(2.3)*
ETP	2.6	0.5
Nematodes, Oligochaetes, & Turbellaria	10.9	0.1
Hydracarina	1.7	2.0
Hemiptera, Coleoptera, & Hymenoptera	0.1	0.2
Mollusca	1.6	0.0

Other (mainly Coelenterata)	28.0	0.1

ETP = Ephemeroptera, Trichoptera, and Plecoptera as a group

Table 2-6. Frequency of occurrence (%) of fish species and average fish community composition (%) among 18 Barrenland study streams, NWT, Canada.

Species	n	Frequency of occurrence	Composition
Slimy sculpin (*Cottus cognatus*)	17	94	34.3
Burbot (*Lota lota*)	16	89	19.4
Arctic grayling (*Thymallus arcticus*)	16	89	39.5
Lake trout (*Salvelinus namaycush*)	7	39	2.9
Northern pike (*Esox lucius*)	2	11	1.3
Lake chub (*Couesius plumbeus*)	2	11	0.4
Round whitefish (*Prosopium cylindraceum*)	1	6	0.3
Ninespine stickleback (*Pungitius pungitius*)	1	6	1.4
Longnose sucker (*Catastomus catastomus*)	1	6	0.4

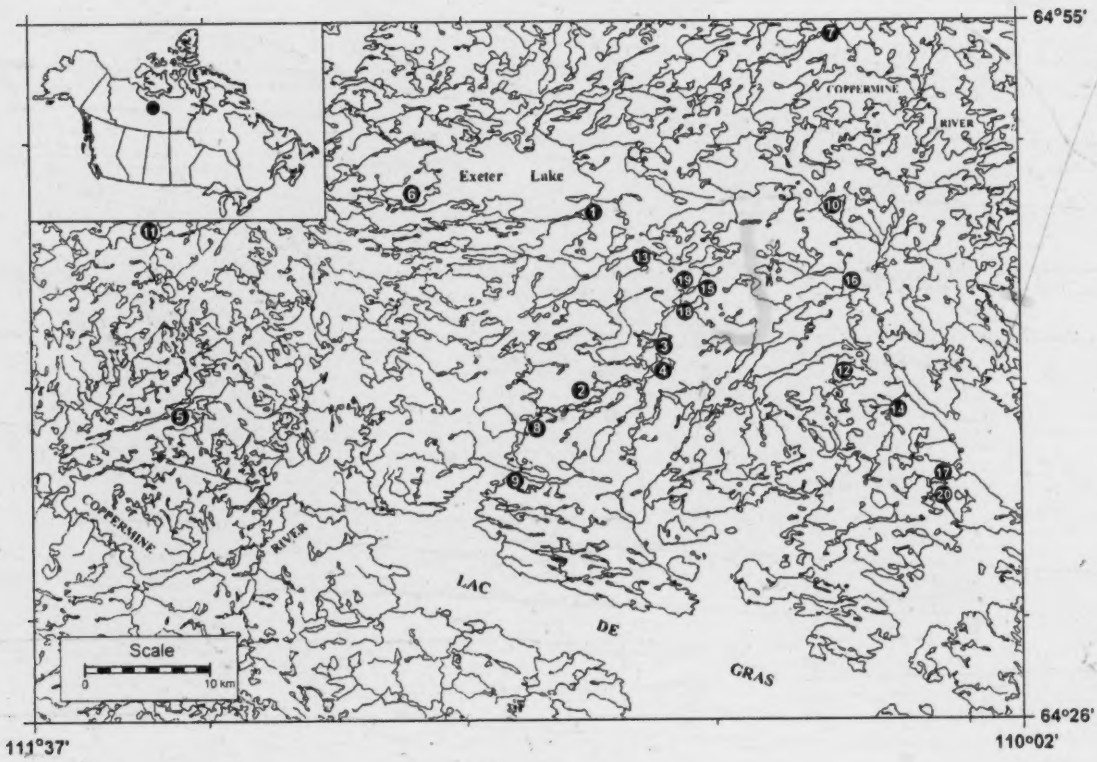

Figure 2-1. Map showing the Lac de Gras study area, with study stream locations indicated by black dots (•). Numbers within dots correspond to streams listed in Table 2-1. Insert: location of study area in the Northwest Territories, Canada.

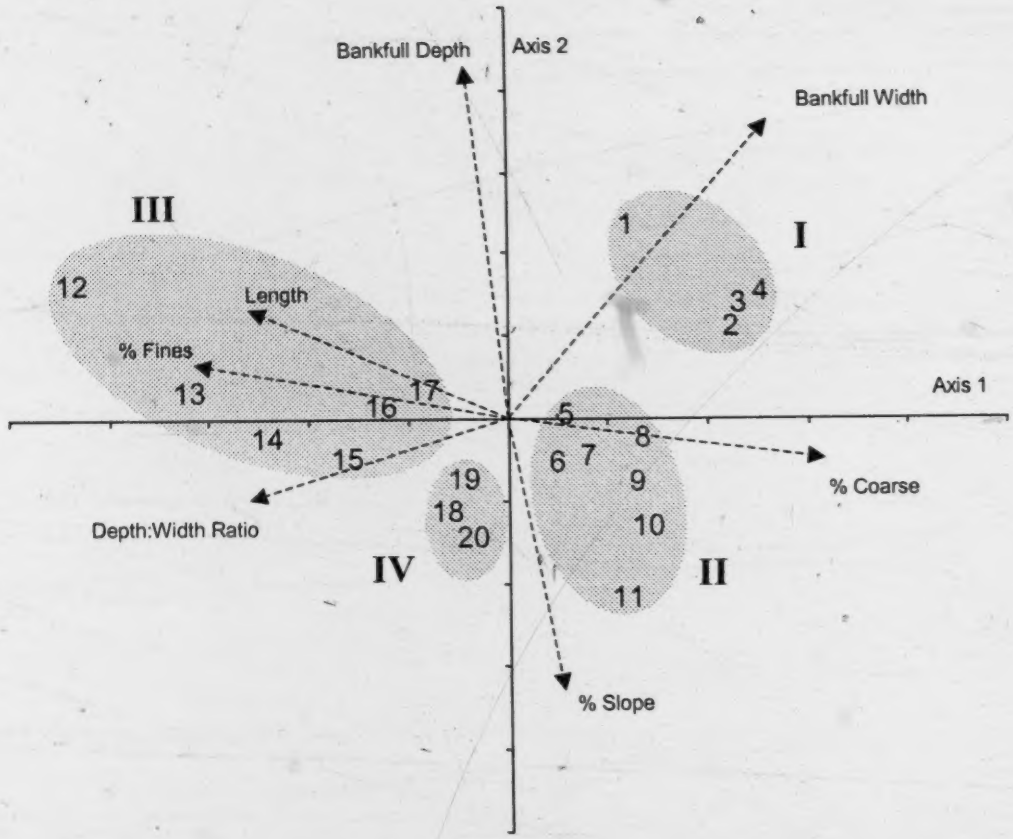

Figure 2-2. Principal components analysis ordination of the 20 study streams (numbered as in Table 1), based on seven physical variables. Vectors (arrows) point in the direction of increasing values for the respective variables, with vector length reflecting the strength of the relationship. Shaded ellipses highlight four groups of physically similar streams (see text for details).

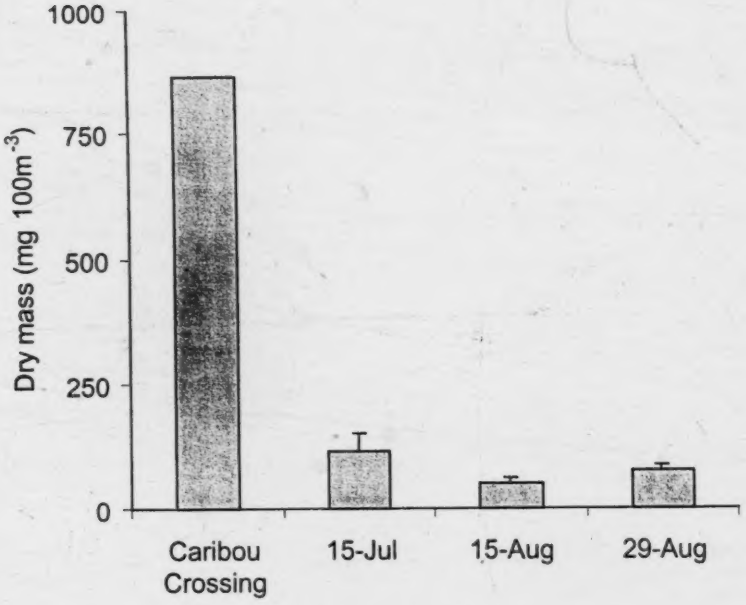

Figure 2-3. Mean ± SE drift biomass found at Polar-Vulture Creek on 12 July, 15 July, 30July, and 29 August 1999. Estimates for each date are based on 18 samples except for the caribou stream crossing estimate (July 12), which is from a single sample collected 30 min. after a herd of ca. 100 caribou crossed Polar-Vulture.

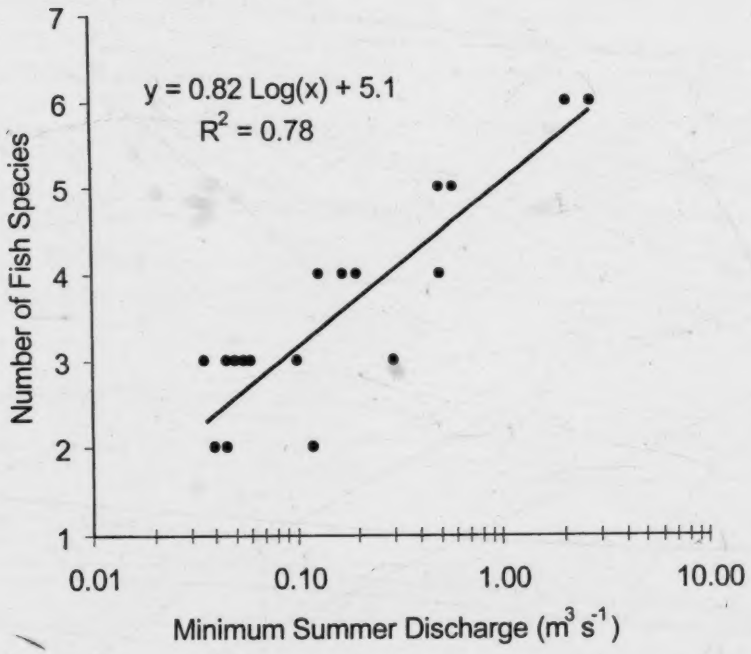

Figure 2-4. Relationship between number of fish species found in 18 study streams and the minimum summer discharge, based on surveys in mid-August, 2000.

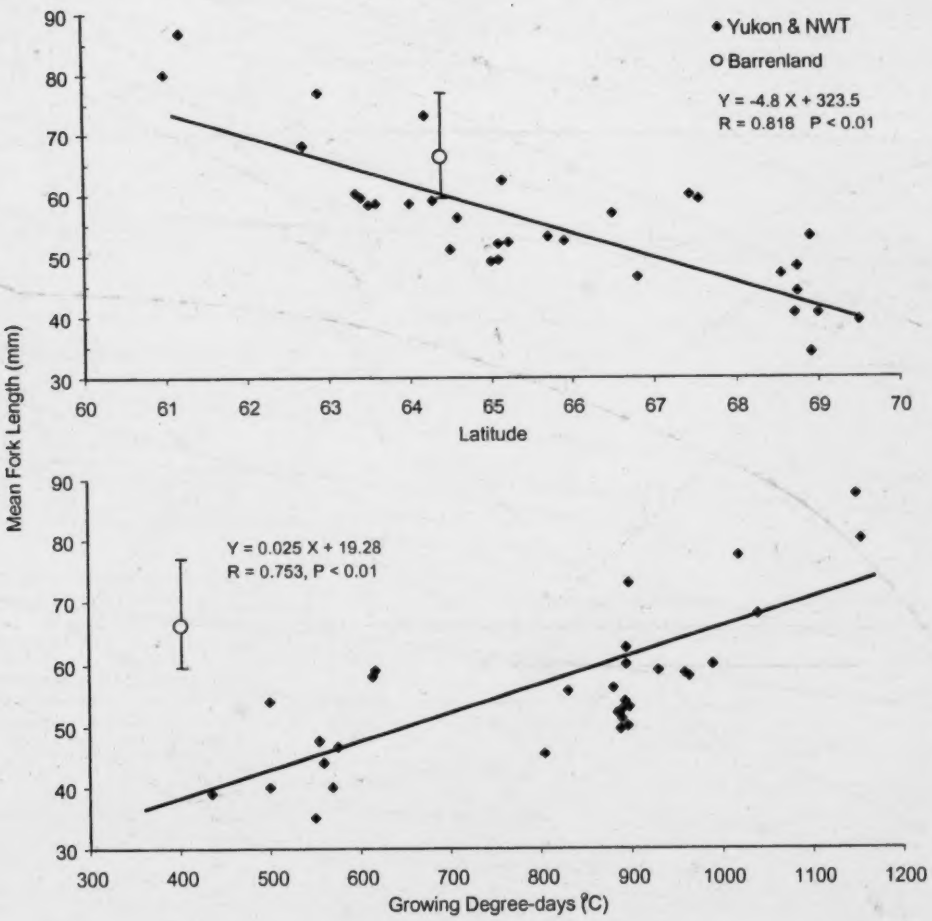

Figure 2-5. Relationships of mean fork length of YOY Arctic grayling in late August to latitude of individual streams (upper) and growing degree-days (5°C) (lower) in north western Canada (black diamonds) and Barrenland streams (open circle). Error bars are ranges from 10 Barrenland streams during 1998-2000. Comparison data and linear regressions are from the Mackenzie Valley and Yukon North Slope drainages (figure modified from McCart, 1986). Barrenland climate data are from Contwoyto Lake, Northwest Territories (65°29'N 110°22'W) (Environment Canada 1991), adjusted to match McCart (1986), who defined growing degree-days from a base of 4.4°C (40°F).

Chapter III: Selective feeding of age-0 Arctic grayling in lake-outlet streams of the Northwest Territories, Canada

Introduction

The landscape of the Barrenlands region of the Northwest Territories, Canada, is dominated by innumerable lakes that are connected to each other in chains by relatively short streams. At ice-out, lake-dwelling Arctic grayling, *Thymallus arcticus*, enter these lake-outlet streams to spawn, and return to the lake shortly thereafter, leaving streams to serve primarily as nursery habitat for the young-of-the-year (YOY) grayling (Chapter II). Growth and survival of young fish depend heavily on the availability of suitable prey at the onset of yolk-sac absorption (Braum 1978) and on the ability of YOY to reach sufficient size during their first growing season (Miller et al. 1988). Thus, the productive capacity (sensu DFO 1986) of Barrenlands streams as habitat for Arctic grayling is derived largely from the ability of streams to provide nourishment for the growth of YOY grayling. Hampering our ability to assess productive capacity of these streams, however, is our lack of knowledge of the food requirements of YOY grayling (Armstrong 1986, Northcote 1995).

Grayling appear to feed primarily from the water column. Studies done in other regions indicate the adult and sub-adult grayling feed primarily on drifting insects in lotic systems, while in lakes, planktivory often prevails (Armstrong 1986, Northcote 1995). Benthic foraging for macroinvertebrates may occasionally become important when

invertebrate density in the water column diminishes (Armstrong 1986). The significance of terrestrial insects that fall onto the waters' surface is not well known, but may vary with stream size and characteristics of the riparian vegetation, both which would influence the abundance of this prey type (Armstrong 1986). Based on our understanding of fish foraging ecology, however, combined with the nature of Barrenland streams, drifting microcrustacea may be important for YOY grayling in these lotic ecosystems.

Although fish are generally size-selective foragers on invertebrates (Werner 1974), the gapes and swimming abilities of YOY fish can limit the sizes of prey that they can capture and consume (Miller et al. 1988, Schael et al. 1991). Because of their lake-outlet characteristics, Barrenland streams are characterized by high drift densities of lake-derived microcrustacea (Chapter II). A reasonable hypothesis, therefore, would be that YOY Arctic grayling are relatively independent of autochthonous production of macroinvertebrates in Barrenland streams but instead primarily depend on lake-derived microcrustacea for nourishment. Furthermore, a lack of extensive, overhanging vegetation should also limit the importance of terrestrial invertebrates as prey of YOY grayling in these tundra streams. To examine these hypotheses, I quantified the relative importance of lake-derived microcrustacea, terrestrial invertebrates, and benthos-derived drifting invertebrates as food for YOY grayling in Barrenland streams. I also determined the relative abundance of these potential prey types in Barrenland streams, which allowed me to address two additional questions: (i) are YOY grayling selective foragers in terms of prey type, prey size, and per life-history stage? (ii) does grayling size affect the size and types of organisms they consume? By quantifying the diets of YOY grayling in

these streams, my study should increase understanding of the factors that contribute to the productive capacity of Barrenland streams as fish habitat.

Methods

The study was centred north of Lac de Gras, ca. 64°45'N, 110°30'W, roughly 100 km north of the tree line. Streams in this region are generally small (bankfull width 2-50 m), and short (length 80-2900 m) lake-outlet systems (Chapter II). Freshet begins in late May and flows (0.1 to 7.0 $m^3 \cdot s^{-1}$) continue until late September, when streams freeze completely. Stream water is circumneutural, stained yellow-brown, and low in turbidity and conductivity (8-19 $\mu s \cdot cm^{-1}$). The streams support modest densities of benthic invertebrate (17,000 $ind. \cdot m^{-2}$), and upstream lakes provide large numbers of microcrustacea, 10,000 $ind. \cdot 100m^{-3}$, to the drift (Chapter II).

Fieldwork was conducted in two streams, Polar-Vulture and Pigeon (Table 3-1). Polar-Vulture contains large substrates and the channel is braided for most of its length. Pigeon has a large amount of fine sediment, particularly sand, and has a single channel for much of its length. The two streams are 10 km apart. The riparian zone of Polar-Vulture is well drained and considerably drier than that of Pigeon. Dwarf heath and scattered low shrub tundra dominates the riparian zone at Polar-Vulture, whereas Pigeon is dominated by sedge tussock.

Young-of-the-year habitat use and foraging behaviour

Stream fish communities are numerically dominated by YOY Arctic grayling, with slimy sculpin, *Cottus cognatus*, and burbot, *Lota lota,* also present. Upon swim-up in early July, grayling are 11-13 mm in length. Foraging begins several days later, often with yolk sacs still visible. Small grayling (< 25 mm in length) use marginal habitats along the

banks, < 25 cm deep and with water velocities < 5 $cm \cdot s^{-1}$. As the YOY grow they become territorial, proficient swimmers, and shift to the main channel (depths > 40 cm and mean water velocities of ca. 15 $cm \cdot s^{-1}$) (N. Jones, unpublished data). At this stage, grayling use velocity refugia associated with pools or created by large boulders along the thalweg and feed opportunistically on drifting organisms.

Field sampling

I sampled young-of-the-year Arctic grayling from Polar-Vulture Creek, two (1998), three (1999) or four (2000) times per summer, between mid- July and late-August, and four times in 2000 from Pigeon Creek. I sampled grayling after they shifted their habitat use to the main channel (fork length > 25 mm). Grayling were collected primarily with dip nets or with a Smith-Root Model A-12 backpack electrofisher when fish became too dispersed to capture otherwise (late summer). I collected grayling shortly after and downstream of the mid-afternoon drift samples (see below). Upon capture, fish were euthanized (Tricane overdose) and preserved in 90% ethanol. In the laboratory, I measured fish fork length (± 0.5 mm) and removed their stomachs.

I sampled drift from Polar-Vulture in 1999 and 2000 and from Pigeon Creek in 2000, just prior to each fish sampling. I sampled drift simultaneously at two locations within the streams with two tri-net samplers (0.25 mm mesh, Field-Dodgson 1985). Samples were collected either immediately above or below riffles in relatively shallow water (mean depth and velocity, 0.16 m and 0.24 $m \cdot s^{-1}$, respectively) and in close proximity to fish collection areas in order to reflect organisms available to grayling. On each sampling date, I collected drift at dawn, noon, and dusk. Nets were wetted for 30 – 45 minute intervals, depending on flow rates, to filter 3 – 6 m^3 of water. To determine

sample volumes, I measured water velocities at the mouth of each sampler using a Swoffer Model 2100 velocity meter. Drift samples were preserved in 70% ethanol and later identified and counted.

Laboratory analyses

Nineteen invertebrate taxa were identified in the drift and stomach samples, and subsequently classified taxa as either large or small based on body size (Table 3-2). Where possible, I also identified insects as larvae, pupae, or adults. Drift samples were subsampled volumetrically in 1999 and 2000, with 63% and 42% of each the sample, on average, examined, respectively. All organisms in the stomach samples were identified and counted. To extend the examination of prey size selection, I measured head capsule widths of the two most commonly consumed invertebrate taxa, Chironomidae and Simuliidae, from random samples of drift and stomachs from each sampling period in 2000. Individuals were measured using a dissecting scope equipped with an ocular micrometer for measurements (± 0.01 mm).

Statistical analyses

I excluded invertebrate taxa that did not comprise at least 5% by number of the drift and stomachs on any date from analyses. To keep them above the 5% criteria, Ephemeroptera, Trichoptera, and Plecoptera (ETP) were grouped in 1998 and 1999. Selectivities by YOY Arctic grayling for each prey group were calculated from Polar-Vulture and Pigeon Creeks in 2000, using the index of preference *D*:

$$D_i = \frac{r_i - p_i}{(r_i + p_i) - 2r_i p_i}$$

where D_i is the index of preference for prey group i, p_i is the proportion of individuals belonging to prey group i in the drift, and r_i is the proportion of the prey group in the stomach (Jacob 1974). Values of D range from –1.0 to 1.0; 0.0 indicates random feeding, while $D > 0.0$ and $D < 0.0$ indicate preference and avoidance, respectively.

I used t-tests to determine if prey selection values differed from zero over the four samplings of 2000. Six prey groups from each stream were tested individually; sample sizes were 120 fish per stream (four samples of 30 fish). To assess if differences in selection strength existed among prey groups, I combined data from both streams and the four sampling periods from 2000 into a general linear model (GLM), following arcsine transformation. Significant GLM results were followed by Tukey multiple comparison tests to identify differences in prey group means. To examine how gape limitation vs. size-selection affected prey selection as a function of fish size, I used linear regression to determine if the numbers of small (mostly microcrustacea) and large invertebrates (mostly insect larvae) and the proportion of large invertebrates in the diets varied with the size of YOY grayling over of the course of the summer. Mann-Whitney U-tests were used to determine if head capsule widths of Chironomidae and Simuliidae, the predominant large invertebrates, differed between stomachs and drift within each stream for each date. Mann-Whitney tests were also used to determine if there were differences in the relative composition of larvae, pupae, and adult Chironomidae and Simuliidae between the drift and diet. For all statistical tests, I used $\alpha = 0.05$ as a critical level of significance (after performing the Bonferroni adjustment, when required, to reduce the experimentwise error rate). I used the Kolmogorov-Smirnov test to examine data for normality and Levene's median test for homogeneity of variances. Proportion data were

arcsine-square root transformed and the numbers of small and large invertebrates in the diets of grayling were log-transformed prior to regression analyses.

Results

Composition of drift and diet

Observations of YOY Arctic grayling indicated that they fed almost exclusively from the water column. Rarely, fish made foraging attempts along the bottom of the stream. Very few of the 358 YOY grayling stomachs examined contained sand or algae that would indicate benthic feeding. Disturbed fish quickly returned to their central place and resumed foraging. Based on these observations, I focused on the drift, rather than benthos, as the source of available prey.

Drift was numerically dominated by microcrustaceans, including cladocerans, copepods, and ostracods (Figure1 and 2). The remaining portion of the drift consisted mostly of dipterans and, to a lesser extent, ETP taxa and mites. In contrast, YOY grayling consumed mainly dipterans, predominantly chironomids and simuliids, but only small numbers of microcrustaceans (Fig. 3-1 and 3-2). Ephemeropterans were common in the diet in July but diminished by August. Both the diet and drift contained small numbers of adult terrestrial insects, particularly Hymenoptera and Culicidae (< 5% by number of the drift and stomachs on any date from analyses). Organic debris was present in 7.5 to 25% of grayling stomachs. All stomachs contained prey items.

Spatiotemporal variation in drift and diet

Although the above pattern was generally consistent among years, the composition of invertebrates in the diet and drift was seasonally variable. For example, dipterans decreased in Polar-Vulture Creek from 37% of the drift to 1% over a 44-day period in

1999 (Fig. 3-1). In that year, which was unusually cold and wet, mites were also more abundant than in other years. In Pigeon Creek (2000), the relative contributions of chironomids and simuliids to the diet increased and decreased, respectively, over the 45-day period (Fig. 3-2). The major difference between the two streams was a higher proportion of simuliids vs. chironomids in Pigeon Creek, as evident in both the drift and diet (Fig. 3-2).

Prey selection

There was a good relationship between prey preference and prey size. In both streams, YOY grayling displayed strong avoidance (t-tests, $P < 0.05$) of small invertebrates (especially microcrustacea, nematodes, and mites), and preferentially consumed chironomids and simuliids (t-tests, $P < 0.05$; Fig. 3-3). Preferences (D) for each of the six prey groups were significantly different from zero, (t-tests, $P < 0.05$). Mean selection values differed for each prey group except for Hydracarina, Crustacea and Nematoda (GLM followed by Tukey multiple comparisons, $F_{5, 1430} = 383$, $P < 0.05$). The general patterns of preference and avoidance among taxa were consistent between streams (GLM, $F_{1, 1430} = 0.02$, $P = 0.965$). However, the relative preferences for midges and blackflies switched between streams, and mites were more strongly avoided in Pigeon Creek (Fig. 3-3). The strength of selection differed among sampling dates, which was primarily driven by a strong selection for ephemeropterans in July followed by little selection in August (GLM, $F_{3, 1430} = 18.79$, $P < 0.05$). The number of both small and large prey in the diets ($n = 240$) increased of as the grayling grew (linear regressions, $R^2 = 0.10$, $P < 0.001$, and $R^2 = 0.32$, $P < 0.001$, respectively), the later increasing at a faster rate than the former (t-test, $P < 0.01$). However, the relative proportion of large invertebrates

remained fairly constant (mean = 90%, SE = 0.9) as fish increased in fork length from ca. 25 to 90 mm ($R^2 = 0.001$, $P = 0.487$).

Even within the preferred prey groups of Chironomidae and Simuliidae, YOY grayling tended to select larger individuals from the drift (Fig. 3-4). Interestingly, however, the mean size of chironomids and simuliids consumed and in the drift did not increase uniformly over the summer (Fig. 3-4), perhaps suggesting multiple cohorts or species-specific differences in availability.

The dipterans in both the drift and stomach contents of YOY grayling were dominated by larval stages (Fig. 3-5). However, grayling consistently consumed a disproportionate number of emerging pupal chironomids and simuliids and, in Pigeon, a disproportionate, though still small, number of adult simuliids (Fig. 3-5).

Discussion

Similar to larger and older grayling in streams of British Columbia and Alaska (Stuart & Chislett 1979, Elliott 1982), I found that drifting macroinvertebrates, primarily chironomids and simuliids, are important prey for YOY Arctic grayling in small streams of the Barrenlands. Furthermore, given the relative availability of prey in these lake-outlet streams, I found that grayling prey selectively on these two groups, whereas large numbers of microcrustacea that drift into stream channels from the upstream lake are avoided, as are other small invertebrates. Terrestrial invertebrates were of limited availability and rarely found in the diet.

Efficient feeders that optimize their net energy gain should have greater growth and reproductive output, and therefore increased fitness, than less efficient feeders (Wootton 1990). As a result, foraging theory predicts that, fish should employ the most profitable

feeding strategies available to them, within constraints, including selection of certain prey types and sizes (Werner 1974). Studies of stream-dwelling salmonids (e.g., Allan 1981, Bannon & Ringler 1986, Keeley and Grant 1997) have documented selection for larger invertebrate groups and larger individuals within such groups. Consistent with this, I observed that YOY grayling avoided the abundant but small zooplankton, whereas the rarer but larger insects, especially chironomids and simuliids, were consumed preferentially. Moreover, I found that grayling tended to select the larger dipterans from the drift. It is unlikely that the zooplankton are too small to be seen or retained by gill rakers of YOY (Wankowski 1979); large adult Arctic grayling readily consume *Daphnia* (O'Brien et al. 2001). It is possible, however, that zooplankton are less detectable than the larger and more darkly colored dipterans. Despite the almost 9-fold difference in the abundance of zooplankton relative to dipterans, the dominance of dipterans in the diet of YOY suggests strongly that such selective foraging results in a greater net energy gain than feeding on microcrustaceans.

Typically, fish ingest larger prey (Wankowski 1979, Werner & Gilliam 1984, Keeley and Grant 1997) and increase diet breadth (Allen 1941, Cadwallader 1975) with increasing body size. However, I found that prey size of YOY grayling varied relatively little over a season. This is likely because the size range of invertebrates available for consumption in these Barrenlands streams was rather restricted, as was the size of fish (YOY from ca. 25 to 90 mm in length). Organisms larger than chironomids and simuliids (e.g., Acrididae, and Coleoptera) were rarely found and were generally very large (ca. 30-40 mm in length and quite wide) such that they probably could not be consumed by YOY grayling due to gape limitation (Schael et al. 1991).

Similarly, the diversity of available prey in my study streams was fairly limited, resulting in YOY grayling having a limited and relatively invariant diet of chironomids and simuliids throughout the summer. Terrestrial prey, in particular, was notably unimportant as food for my YOY Arctic grayling. In 1999, however, a wet and cool summer, mosquitoes were abundant in riparian areas, and were disproportionately more abundant in YOY stomachs (15% by number) compared to that in the drift (7% of all individuals). Otherwise, terrestrial insects were not often consumed, nor readily available, even though they are often an important food elsewhere, particularly in small streams with dense riparian vegetation (Armstrong 1986).

Elliott (1982) found that diet diversity increased among older and larger grayling, including the consumption of terrestrial prey, while YOY largely concentrated on aquatic organisms. This was also found in a seasonal analysis of the diet and feeding dynamics of brown trout (*Salmo trutta*) in the Owenddoher Stream, Ireland (Kelly-Quinn and Bracken1990). In fact, Elliott (1982) found that the number of terrestrial insects in the diet surpassed the number of aquatics in some streams. Elliott (1982) suggested that the trend of increasing diet diversity is a function of several factors, including more prey becoming available as fish grow and are able to consume larger prey organisms and because larger fish are able to use a broader range of stream habitats as they grow and become stronger swimmers. Thus, the paucity of terrestrial and other large prey consumed by YOY grayling in Barrenlands streams may also reflect their small size, rather than (or in addition to) differences in prey availability and preference.

Ephemeropterans, although comparable in size to chironomids and simuliids, were not preferentially selected. Because ephemeropterans were much lower in abundance

compared to chironomids and simuliids, grayling were perhaps more familiar with the shape and drifting behaviour of these dipterans and thus may have developed a 'training bias' (sensu Dill 1983). The low predation intensity on ephemeropterans could also be the result of decreased catchability and increased handling time required to consume a more motile and behaviorally responsive insect (Scrimgeour et al. 1994). Though perhaps not as important in the Arctic summer, mayflies are also well known to reduce the risk of predation by drifting at night when predatory fishes are less likely to detect their presence (Flecker 1992).

The Arctic grayling in my study displayed a sit-and-wait, central-place mode of foraging (Fausch 1984, Grant et al. 1989). This mode is well suited for preying on drifting insect larvae, emerging pupae, and surface oriented adults, but not cryptic, stationary benthic prey. Relative to the abundances of the three insect stages, pupae were selected preferentially. Pupation emergence is a vulnerable time in the life cycle of an aquatic insect (LaFontaine 1981).

Individual variation among trout is frequently noted in diet studies (Allan 1981, Ringler 1983). Although rare, I found some grayling consumed high numbers of certain prey, including crustacea, mayflies, wasps, and mosquitoes, that were normally taken in low numbers. Such variation may be related to individual hunger level, past feeding experience or represent opportunistic feeding such as when wind-downed insects become available or when migrating caribou cause catastrophic drift by the benthic invertebrate community (Chapter II). Discovering the mechanism(s) behind this individuality is an interesting challenge, however, such variation was inherently exceptional in my study

streams and most grayling mainly consumed chironomids and simuliids in a truly selective manner.

Our understanding about northern aquatic resources remains very much incomplete (Schindler 2001, NSERC 2001), yet is critical for the protection and management of those resources. This study contributes to our understanding of the food habits of YOY Arctic grayling, an economically and culturally important, yet poorly understood, fish species in Canada's North. As well, this study demonstrates clearly that despite the abundance of lake-derived zooplankton in the lake-outlet streams of the Barrenlands, productive capacity of these streams will likely remain dependent on instream production of invertebrates. As resource exploitation increases in the Arctic regions of the world so to will the unavoidable alteration, disruption, and destruction of fish habitat (sensu DFO 1986). Habitat compensation efforts will need to provide more than just suitable physical habitat for fish, but must also consider autochthonous invertebrate production.

Literature Cited

Allan, J.D. 1981. Determinants of diet of brook trout (*Salvelinus fontinalis*) in a mountain stream. Can. J. Fish. Aquat. Sci. 38:184-192.

Allen, K.R. 1941. Studies on the biology of early stages of the salmon (*Salmo salar*). J. Anim. Ecol. 10: 47-76.

Armstrong, R.H. 1986. A review of Arctic grayling studies in Alaska, 1952 – 1982. Biological Papers of University of Alaska. Number 23. pp. 3-17.

Bannon, E. & N.H. Ringler. 1986. Optimal prey size for stream resident brown trout (*Salmo trutta*): tests of predictive models. Can. J. Zool. 64: 704-713.

Braum, E. 1978. Aspects of the survival of fish eggs, embryos, and larvae. pp. 102-131. In: S.D. Gerking (ed.) Ecology of freshwater fish production. John Wiley & Sons, New York.

Cadwallader, P.L. 1975. The food of the New Zealand common river galaxies, *Galaxias vulgaris* Stokel (Pisces: Salmoniformes). Austr. J. Mar. Freshw. Res. 26: 15-30.

Department of Fisheries and Oceans (DFO) 1986. The Department of Fisheries and Oceans Policy for the Management of Fish Habitat. Department of Fisheries and Oceans, Ottawa, ON. 28 pp.

Dill, L.M. 1983. Adaptive flexibility in the foraging behavior of fishes. Can. J. Fish. Aquat. Sci. 40: 398-408.

Elliott, G.V. 1982. Final report on the evaluation of stream crossings and effects of channel modifications on fishery resources along the route of the trans-Alaska pipeline. U.S. Fish and Wildlife Service, Special Studies, Anchorage, Alaska, USA. 110 pp.

Fausch, K.D. 1984. Profitable stream positions for salmonids: relating specific growth rate to net energy gain. Can. J. Fish. Aquat. Sci. 62: 441-451.

Field-Dodgson, M.S. 1985. A simple and efficient drift sampler. New Zeal. J. Mar. Freshw. Res. 19: 167-172.

Flecker, A.S. 1992. Fish predation and the evolution of diel drift periodicity in aquatic insects: evidence from neotropical streams. Ecology 73: 438-448.

Grant, J.W.A., D.L.G. Noakes, & K.M. Jonas. 1989. Spatial distribution of defence and foraging in young-of-the-year brook charr, *Salvelinus fontinalis*. J. Anim. Ecol. 58: 773-784.

Jacobs, J. 1974. Quantitative measurement of food selection: a modification of the forage ratio and Ivlev's electivity index. Oecologia 14: 413-417.

Keeley, E.R. & J.W.A. Grant. 1997. Allometry of diet selectivity in juvenile Atlantic salmon (*Salmo salar*). Can. J. Fish. Aquat. Sci. 54: 1894-1902.

Kelly-Quinn, M, & J.J. Bracken. 1990. A seasonal analysis of the diet and feeding dynamics of brown trout, *Salmo trutta* L., in a small nursery stream. Aquaculture and Fisheries Management 21: 107-124.

LaFontaine, G. 1981. Caddisflies. Nick Lyons Books, New York. pp. 336.

Miller, T.J., L.B. Crowder, J.A. Rice. & E.A. Marschall. 1988. Larval size and recruitment mechanisms in fishes: toward a conceptual model. Can. J. Fish. Aquat. Sci. 45:1657-1670.

Northcote, T.G. 1995. Comparative biology and management of Arctic and European grayling (Salmonidae, Thymallus). Rev. Fish Biol. Fish.5:141-194.

NSERC (National Science and Engineering Research Council of Canada). 2000. From crisis to opportunity: Final report to NSERC and SSHRS from the task force on northern research. National Science and Engineering Research Council of Canada and Social Sciences and Humanities Research Council of Canada. Cat. No. NS3-31/2000.

O'Brien, W.J., M. Barfield, & K. Sigler. 2001. The functional response of drift-feeding Arctic grayling: the effects of prey density, water velocity, and location efficiency. Can. J. Fish. Aquat. Sci., 58: 1957-1963.

Ringler, N.H. 1983. Variation in foraging tactics of fishes. pp. 159-171. In: D.L.G. Noakes, D.G. Lindquist, G.S. Helfman & J.A. Ward (ed.) Predators and Prey in Fishes, Dr. W. Junk, The Hague.

Schael, D.M., L.G. Rudstam, & J.R. Post. 1991. Gape limitation and prey selection in larval yellow perch (*Perca flavescens*), freshwater drum (*Aplodinotus grunniens*), and black crappie (*Pomoxis nigromaculatus*). Can. J. Fish. Aquat. Sci.. 48: 1919-1925.

Schindler, D.W. 2001. The cumulative effects of climate warming and other human stresses on Canadian freshwaters in the new millennium. Can. J. Fish. Aquat. Sci., 58: 18-29.

Scrimgeour, G. J., J.M. Culp, & K.J. Cash. 1994. Anti-predator responses of mayfly larvae to conspecific and predator stimuli. J. N. Am. Benth. Soc. 13: 299-309.

Stuart, K. M. & G. R. Chislett. 1979. Aspects of the life history of the Arctic grayling in the Sukunka drainage. Prepared by British Columbia Fish and Wildlife Branch, Prince George, British Columbia, Canada. 111 pp.

Wankowski, J.W.J. 1979. Morphological limitations, prey size, and growth response of juvenile Atlantic salmon, Salmo salar. J. Fish Biol. 14: 89-100.

Werner, E.E. 1974. The fish size, prey size, handling time relation in several sunfishes and some implications. J. Fish. Res. Board Can. 31: 1531-1536.

Werner, E.E. & J.F. Gilliam. 1984. The ontogenetic niche and species interactions in size-structured populations. Ann. Rev. Ecol. Syst.15: 393-425.

Wootton, R.J. 1990. Ecology of teleost fishes. Chapman & Hall Ltd., New York. USA. 386 pp.

Stream	Length (m)	Slope %	Bankfull width (m)	Bankfull depth (m)	Mean velocity (ms^{-1})	% fines[a]	% coarse[a]
Polar-Vulture	700	1.4	2.7	0.44	0.13	20	55
Pigeon	2900	0.5	2.4	0.46	0.16	30	58

Table 3-1. Physical characteristics of Polar-Vulture and Pigeon streams, Northwest Territories, Canada.

[a] fines includes clay, silt, and sand (< 2 mm), and coarse includes cobble and boulder (64 – 256 mm).

Table 3-2. Invertebrate taxa identified in the stomachs of YOY Arctic grayling and drift samples collected from Polar-Vulture (1998-2000) and Pigeon (2000) streams. Invertebrates were classified as large or small based on body size. In 2000, Diptera were divided into Chironomidae, Simuliidae, and Culicidae. For some analyses, Cladocera, Copepoda, and Ostracoda were grouped together (as microcrustacea), as were Ephemeroptera, Plecoptera, and Trichoptera (as ETP). Where possible, insects were identified as larvae, pupae, and adult.

Large invertebrates		Small invertebrates	
Diptera	Plecoptera	Cladocera	Oligochaeta
Chironomidae	Hemiptera	Copepoda	Collembola
Simuliidae	Trichoptera	Ostracoda	Tardigrada
Culicidae	Coleoptera	Hydracarina	Coelenterata
Ephemeroptera	Hymenoptera	Nematoda	

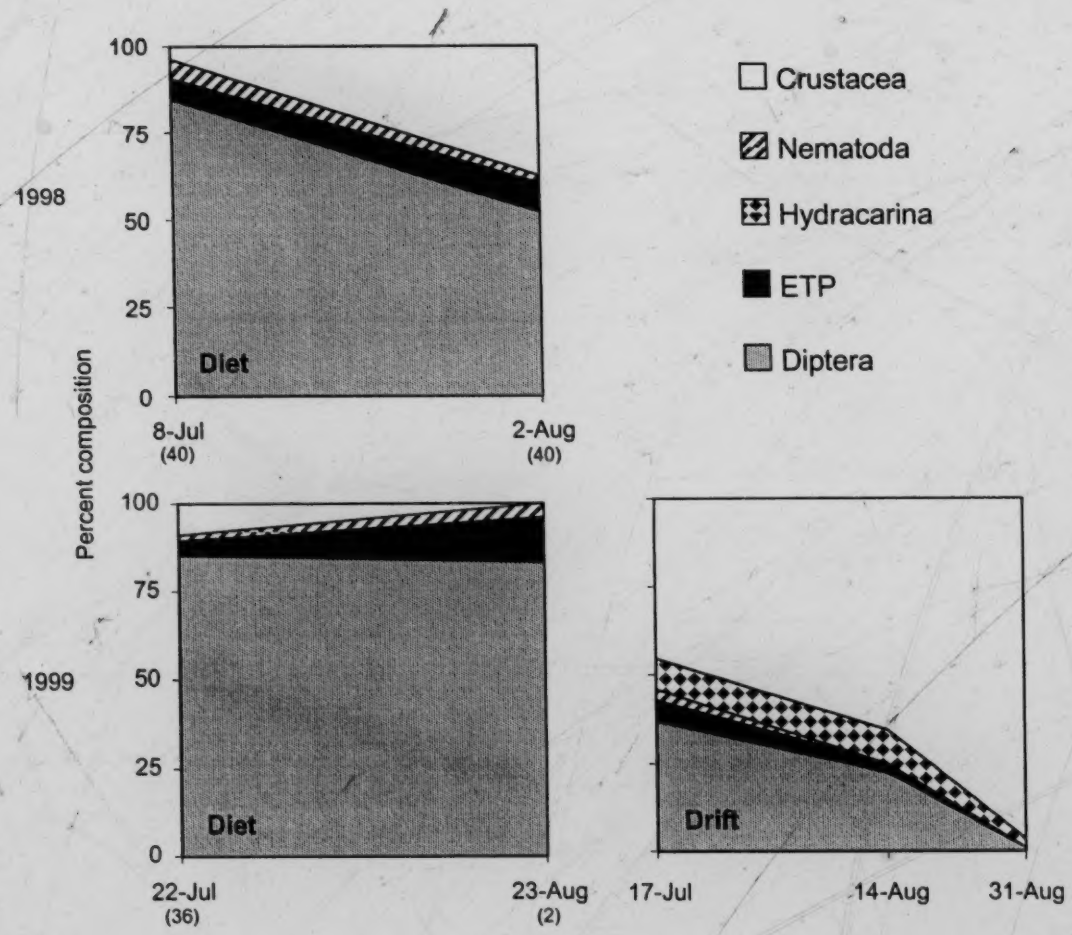

Figure 3-1. Percentage composition of invertebrates in the drift and diet of young-of-the-year Arctic grayling and drift during summers 1998 (upper) and 1999 (lower) in Polar-Vulture Creek. Ephemeroptera, Trichoptera, and Plecoptera, (ETP) were grouped. Number of stomachs examined for diet analyses are given in parentheses. Eighteen drift samples were collected per date.

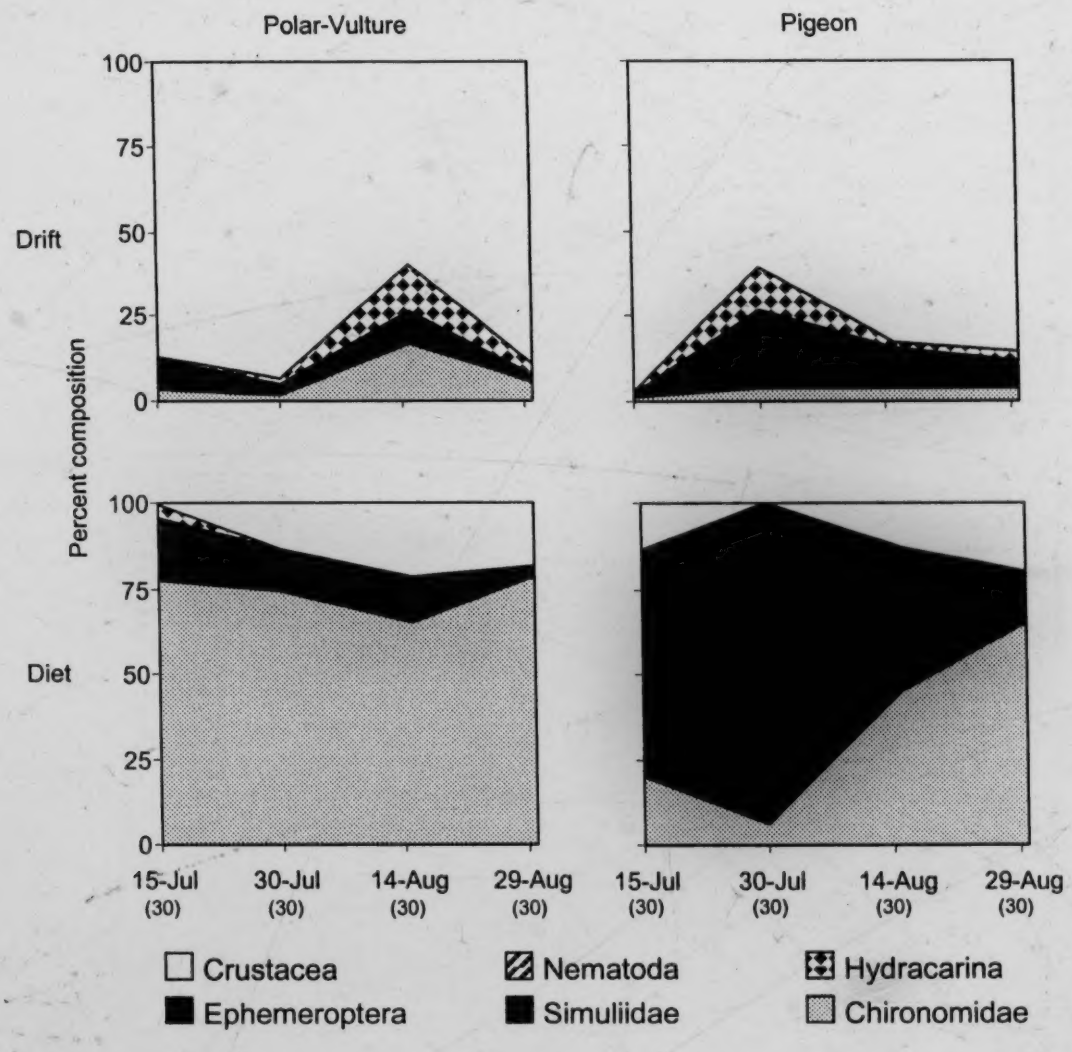

Figure 3-2. Percentage composition of invertebrates in the diet of young-of-the-year Arctic grayling and drift from Polar-Vulture and Pigeon Creeks in 2000. Number of stomachs examined for diet analyses are given in parentheses. Eighteen drift samples were collected per date.

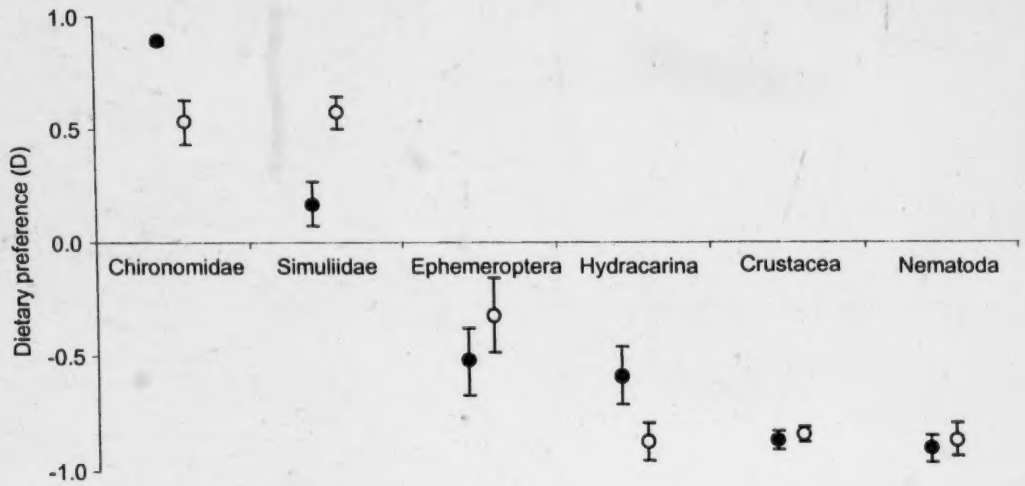

Figure 3-3. Mean (± 95% confidence interval) dietary preference (Jacob's D) by young-of-the-year Arctic grayling from Polar-Vulture (solid circles) and Pigeon Creeks (open circles) in 2000. Positive values indicate preference and negative values indicate avoidance. Prey taxa are arranged left to right by decreasing size. Sample size was 120 stomachs per stream (i.e., 4 samples of 30 fish).

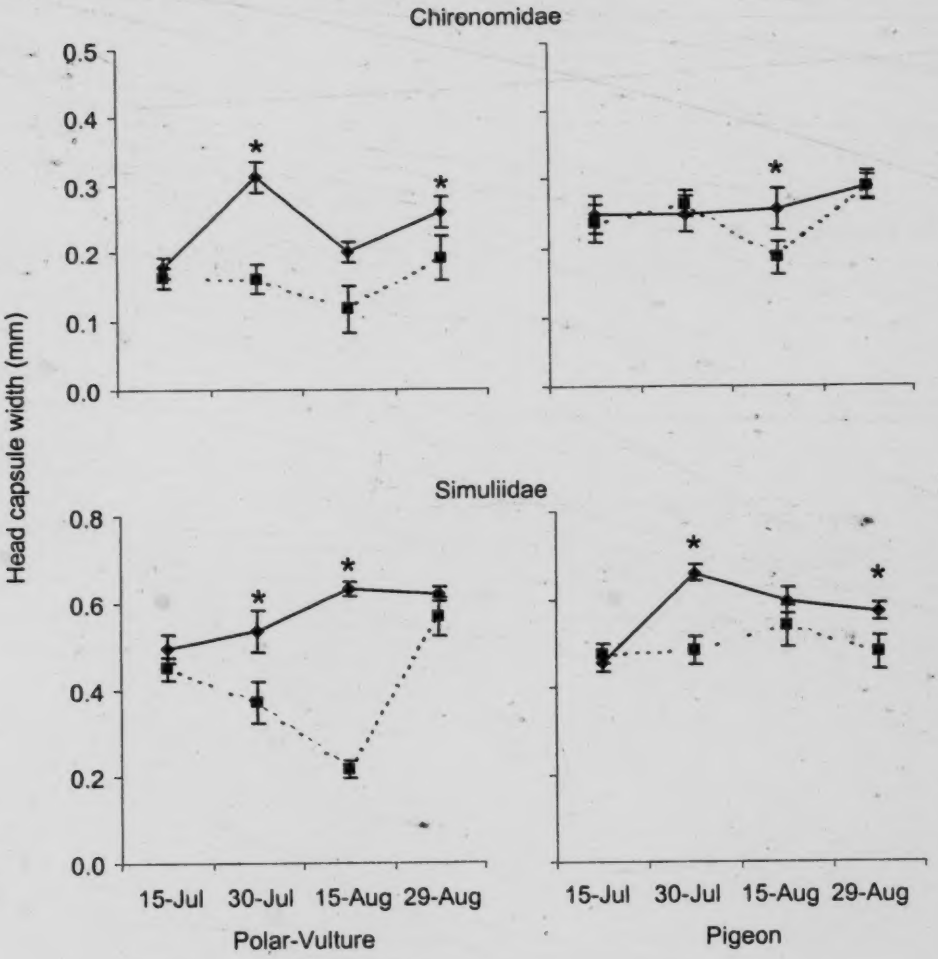

Figure 3-4. Mean (± SE) head capsule widths of larval Chironomidae (upper) and Simuliidae (lower) in the drift (squares) and diet of young-of-the-year Arctic grayling (diamonds) in Polar-Vulture (left) and Pigeon creeks (right), July-August 2000. Significant differences (Mann-Whitney tests, $P < 0.05$; with Bonferroni adjustment) are indicated with an asterisk. Average sample size per date is 22.

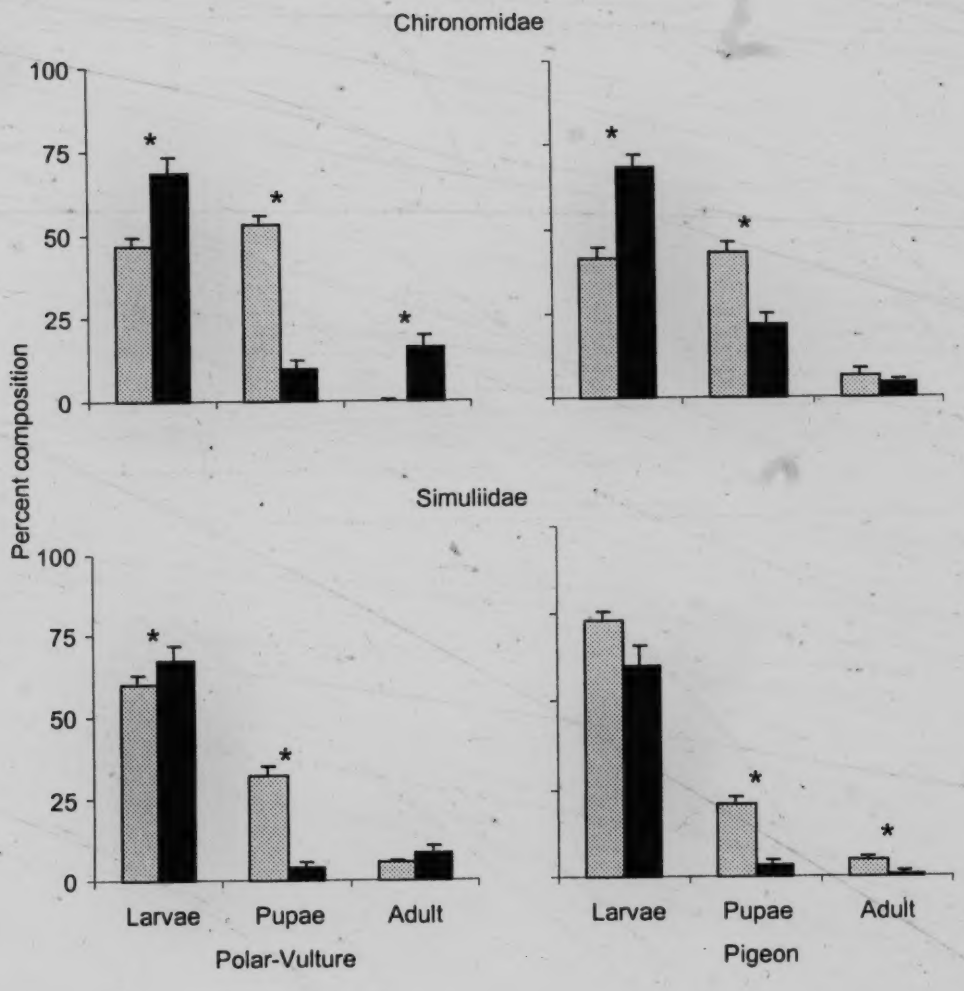

Figure 3-5. Mean (± SE) percentage composition of different life history stages of Chironomidae (upper) and Simuliidae (lower) in the diet of young-of-the-year Arctic grayling (grey) and drift (black) from Polar-Vulture and Pigeon creeks during July-August, 2000. Significant differences (Mann-Whitney tests, $P < 0.05$; with Bonferroni adjustment) are indicated with an asterisk. Sample sizes for Polar-Vulture are 72 and 120, and for Pigeon are 66 and 123, for drift and stomach samples, respectively.

Chapter IV: Productive capacity of an artificial stream in the Canadian Arctic: assessing the effectiveness of compensation

Introduction

Habitat loss and degradation caused by extraction of natural resources, industrial processing, agriculture, and urbanization threaten the sustainability of fisheries resources. In Canada, the principle legislation for the conservation and management of fisheries and fish habitat is the Fisheries Act. Under this Act, management strategies focus on preventing the harmful alteration, disruption, or destruction (HADD) of habitats that sustain fish productivity. To guide implementation of the Act, the Department of Fisheries and Oceans (DFO) developed a "Policy for the Management of Fish Habitat" (hereafter, the Policy, DFO 1986). The guiding principle of the Policy is to ensure "no net loss of productive capacity of fish habitats" (NNL, Minns et al. 1996). Productive capacity is defined in the Policy as "the maximum natural capability of habitats to produce healthy fish ... or to support or produce aquatic organisms upon which fish depend" (DFO 1986, p. 28). When developments that will alter fish habitat are proposed and compensation programs are required, HADD and NNL assume the ability to quantify effects on fish production. This, in turn, presumes that the habitat needs of species are understood, that the relationship between habitat and fish production are known or can be assessed, and that there is an undisturbed natural area or time prior to disturbance that can serve as a reference and provide a measure of the effectiveness of restorative or

enhancement measures (Minns 1997). Frequently, however, one or more of these presumptions are not met. For a variety of reasons, most assessments of habitat compensation must rely on rather indirect measures of program effectiveness (Minns 1997).

Despite the overwhelming importance of NNL to fisheries management in Canada, few studies have evaluated the effectiveness of mitigation measures within this framework. Minns et al. (1996) challenged the scientific rigor of habitat compensation programs and suggested that many are rushed within uncharted ecological territory. Rapid compensation action is often seen as more important than carefully examining alternative avenues of compensation and their eventual effectiveness. Ecological restoration is an emerging science and successful restoration is a serious test of our ecological understanding; as such, efforts will be fraught with mistakes (Bradshaw 1996). A more rigorous approach to compensation is needed, grounded in the principles of the scientific method, including the use of appropriate reference sites. Peer-reviewed examinations of restoration efforts, both successes and failures, need to be published (Bradshaw 1996; Minns et al. 1996), for only then we can begin to learn from our collective experiences.

In 1991, diamonds were discovered in the remote region of the Northwest Territories known as the Barrenlands. In preparation for mineral extraction, two lakes and their tributary streams within a larger chain of lakes were drained. As part of the habitat compensation agreement, a 3.4-km artificial stream was blasted out of Shield rock. Since 1997, water has been diverted around the two lakes, now open-pit mines, through the artificial stream. The objective of the compensation was to restore watershed

connectivity for fish migration and provide spawning and nursery habitats, primarily for Arctic grayling (*Thymallus arcticus*), and thus offset the losses in stream habitat from development.

I based the assessment of this compensation project on a hierarchical framework of the specific functions needed by the artificial stream to achieve no-net-loss of productive capacity. Because I lacked an ecological description of the streams lost during development, or even of Barrenland streams in general, the use of natural, undisturbed streams was all the more important for establishing reference conditions and quantifying gains and losses in productive capacity of fish habitat. The relative simplicity of the fish assemblages and the availability of many pristine streams in the region to serve as reference sites provided an unparalleled opportunity to examine the effectiveness of the artificial stream in providing productive fish habitat, as per DFO's guiding principal of no-net-loss. As part of this examination, the main objectives of my study were to (i) assess the production of young-of-the-year (YOY) grayling in the artificial stream, relative to natural (reference) streams, in terms of density, growth, and condition, and (ii) examine factors that might explain differences in growth between the natural and artificial streams, including water temperature, invertebrate food availability, and physical habitat. I assessed the relative effect of temperature on growth and explored potential effects of food using a bioenergetics model calibrated to field data on YOY Arctic grayling.

Study System

The 4000 km^2 study area is centred around 64°45'N and 110°30'W (see Fig. 4-1), about 100 km north of the tree-line within the southern arctic ecozone. The mean annual

temperature is approximately –12 °C, with a summer maximum of 27 °C and a winter minimum of –54 °C (Environment Canada 1991). The climate is semi-arid with 200–300 mm precipitation annually, 50% of which falls as snow. The region is underlain by granite, gneiss, and schist that form broad, sloping uplands, plateaus, and lowlands. The permafrost layer is continuous. Eskers, kames, and boulder-strewn till plains cover the land. Thin soils in upland areas support dwarf-heath and scattered low-shrub tundra, whereas lowland and depressional areas near lakes and streams are characterized by sedge tussock and low/tall shrub tundra.

The combination of relatively low topographical relief (~50 m) and extensive glacial activity has molded a landscape covered by approximately 21% water in the form of numerous chains of lakes and connecting streams. Following spring runoff, evaporation from lakes gradually lowers lake levels and stream flows diminish, with many small streams eventually becoming dry. Flows can increase (or resume) in late summer and fall, but are frozen solid during the long arctic winter. At approximately 450 masl, the streams of this area are the headwaters of the Coppermine, Back, and Burnside Rivers, which flow north to the Arctic Ocean.

Arctic grayling is well represented in the fish communities, which also include slimy sculpin (*Cottus cognatus*), burbot (*Lota lota*), round whitefish (*Prosopium cylindraceum*), lake trout (*Salvelinus namaycush*), longnose sucker (*Catastomus Catastomus*), ninespine stickleback (*Pungitius pungitius*), lake chub (*Couesius plumbeus*), and northern pike (*Exos lucius*). Most streams support at least one species, but commonly contain only three species: Arctic grayling, burbot, and slimy sculpin (Chapter II). Streams are used mainly for spawning and subsequently as nursery habitat for YOY grayling, whereas the

numerous lakes in the region are used by all ages and species of fish for overwintering. Fish are known to migrate among lakes and streams during the open-water season (N.E. Jones, unpublished data).

Methods

General sampling design

Data were collected during four summers, 1998 to 2001. Twenty natural streams, distributed throughout the study area and ranging in abiotic and biotic conditions, were surveyed for basic physical characteristics, fish community composition and abundance, and the size of YOY grayling just prior to out-migration (Chapter II). Reference streams were selected based on the presence of visible water in the stream channel during aerial surveys in late July. A subset of nine natural streams, more centrally located around the artificial stream, were also sampled for benthic invertebrates, water chemistry, woody debris volumes, substrate coarse particulate organic matter (CPOM), and epilithon; two of these streams, Polar-Vulture and Pigeon, were subjected to more intensive fisheries and invertebrate drift investigations. Given their remote arctic location, reference streams were assumed to represent the range of natural structure and function (e.g., production of YOY grayling) for streams in this region. As such, I used reference streams to establish standards against which differences of the artificial stream could be compared. The artificial stream was sampled for all the above parameters.

Basic stream surveys (stream physical characteristics and fish)

Stream geomorphology, including stream length, slope, bankfull width and depth, and substrate composition, was determined from ground surveys, aerial photographs, and topographic maps. Substrate composition and aquatic vegetation cover were quantified

along several transects perpendicular to stream flow, with substrates classified as clay and silt (< 0.0625 mm), sand (0.0625 – 2 mm), small gravel (2 – 32 mm), large gravel (32 – 64 mm), cobble (64 – 256 mm), and boulder (> 256 mm). Mesohabitat composition (cascade, riffle, run, flat, pool, wetland, boulder garden, and culvert; OMNR 1987) was also quantified as % length of stream.

Arctic grayling fry were first observed 21 to 24 days after spawning (early July). Swim-up dates, determined as the date on which larval grayling were visible along stream margins and captured in larval drift nets, were similar among streams. At this time, young were 11 to 13 mm in length and 0.01 g in mass (Chapter II). During the arctic fall, approximately late August to early September, fish, including YOY grayling, migrate out of streams to overwinter in lakes before streams freeze solid. Hence, by late August, about 50 days after swim-up, YOY grayling mean mass represents a significant percentage of first year growth.

Fish community composition and the end-of-season size of YOY grayling were determined by electrofishing in late summer (about 23 August), shortly before the out-migration, in one, two, ten, and three natural streams in 1998, 1999, 2000, and 2001, respectively. Captured fish were identified, enumerated, weighed (± 0.01 g) and measured (fork length ± 1 mm).

Benthic stream surveys (limnology, woody debris, epilithon, CPOM, and benthic invertebrates)

Three replicate water samples were collected from each stream in late July. Samples were stored in a cold, light-free environment until analysis. In the laboratory, total nitrogen was determined using the persulfate digestion method on a Technicon

Autoanalyzer. Total phosphorus (± 1 $\mu g \cdot L^{-1}$) was determined spectroscopically using persulfate–oxidized samples by molybdate blue absorption.

Woody debris volumes were determined by counting all woody debris longer than 10 cm along 40 - 150 m lengths of stream channel. The mean diameter of wood pieces was determined by averaging the diameters at each end, whereas the length of each piece was the distance between the two ends. These measurements were then used to calculate volume estimates. The surface area of the sampled section of was determined by multiplying the transect length by the mean stream width measured at four locations along the stream. Volumes were then standardized to $cm^3 \cdot 100\ m^{-2}$.

Numbers of shrub stems located within 1 m of the stream bank were counted along transects 40 - 150 m along each stream bank and converted to mean densities ($ind. \cdot m^{-2}$). Transects were also used to quantify the amount of grass and shrubs along stream banks as a percentage of the ground covered, and similarly determined coverage of the streambed by aquatic macrophytes and bryophytes.

Five replicate samples of substrate CPOM, epilithon, and benthic invertebrates were collected in late July from the same locations in both riffles (mean depth and velocity, 0.24 m and 0.25 $m \cdot s^{-1}$) and pools (mean depth and velocity, 0.34 m and 0.08 $m \cdot s^{-1}$). CPOM samples were collected by inserting a plastic jar, 90 mm deep by 80 mm diameter, vertically into the substratum. Within 48 h, I washed the refrigerated samples, removing inorganic material and invertebrate cases and exuviae, and sieved through 1 mm mesh. Filtered organics on the screen were then dried to constant mass at 40 °C (± 0.1mg). Periphyton samples were scraped from the upper surfaces (4.9 cm^2 or 9.6 cm^2) of randomly selected stones. Invertebrates visible without the aid of magnification were

removed from scrapings. Samples were stored frozen in the dark for 2 - 4 weeks before being dried at 40 °C, weighed, ashed at 550 °C, and reweighed for ash-free dry mass determination (± 0.1 mg). Benthic invertebrate samples were collected using a 0.093 m^2 Surber sampler, fitted with a 250 μm mesh. All samples were preserved with 70% ethanol in the field. Invertebrates were identified to genus or species, with the exception of Nematoda, Turbellaria, and terrestrial invertebrates, which were typically identified to Family or Order. Following enumeration, samples were dried to constant mass at 40 °C and weighed (± 0.1 mg).

Intensive stream sampling (temperature, drift, fish growth, biomass, and density)

HOBO temperature loggers synchronously recorded stream water temperature (± 0.1 °C) every four hours from freshet to late August in the artificial (five locations), Polar-Vulture, and Pigeon (two locations each) streams.

The amount and composition of cover available for YOY grayling were visually estimated using transects perpendicular to the axis of the stream. The streams were divided into 10 m sections and a transect was placed randomly within each section. Cover types, which provide one or a combination of velocity refuge, visual isolation or overhead cover (sensu Fausch 1993), included depth, turbulence, rock, undercut, aquatic vegetation, and terrestrial vegetation.

Drift was sampled simultaneously at two locations within each stream with Field-Dodgson tri-net samplers, fitted with 250 μm nets. On each sampling date (15 and 30 July, 15 and 29 August), drift was collected at dawn, noon, and dusk. Samples were collected from relatively shallow water (mean depth and velocity, 0.16 m and 0.24 $m \cdot s^{-1}$, respectively) in close proximity to fish collection areas to reflect organisms available to

grayling. Nets were wetted for 30 – 45 min, depending on flow rates, to filter 3 – 6 m^3 of water. To determine sample volumes, I measured water velocities at the mouth of each sampler using a Swoffer Model 2100 current velocity meter. Drift samples were preserved in 70% ethanol and later identified and counted. Following enumeration, samples were dried to constant mass at 40 °C and weighed (± 0.1 mg).

Invertebrates in the drift were classified as either large (e.g., insects) or small (e.g., microcrustaceans) based on body mass. Head capsule width (± 0.01 mm), an indicator of invertebrate body mass, was measured on Chironomidae and Simuliidae larvae from a random subset of drift samples from each date in year 2000 using a dissecting scope equipped with an ocular micrometer.

In the artificial and Polar-Vulture streams, I estimated total fish density (fish•m^{-3}) and biomass (g•m^{-3}) in late July 1998 - 2000 using the three-pass removal method, with habitat stratified as pools and riffles. Captured fish were identified, enumerated, weighed (± 0.01 g), and measured (fork length ± 1 mm). Volumes electrofished were determined for each section shortly after being surveyed. Computations for population estimates were made separately for Arctic grayling (juvenile and YOY), slimy sculpin, and burbot. For each section of stream, I estimated total fish biomass per species by multiplying the mean individual mass by the number of fish estimated for that section. Upwards of 75% of the estimated total fish abundance were typically captured in each fished section of stream.

Aside from the estimates of first year growth of YOY Arctic grayling prior to out-migration (see Basic stream surveys), the mean mass of YOY grayling was also determined several times from swim-up to shortly before out-migration in the artificial, Polar-Vulture, Pigeon, and Polar-Panda streams.

Finally, the diet of YOY grayling from the artificial stream was determined using methods outlined in Chapter III; briefly, nineteen invertebrate taxa were identified in the stomachs, and subsequently classified as either large or small based on body size. To examine prey size selection, head capsule widths were measured on the two most commonly consumed invertebrates taxa, Chironomidae and Simuliidae, from random subsets of stomach samples from each sampling period in 2000. A dissecting scope equipped with an ocular micrometer was used for measurements (± 0.01 mm). I have included some reference stream data from Chapter III for a comparison with the food habits of YOY grayling from the artificial stream.

Bioenergetic model and simulations

I used bioenergetics modelling to assess the relative effects of different water temperatures in artificial and natural streams on observed growth of YOY Arctic grayling (see Ries and Perry 1995; Railsback and Rose 1999). I used the Wisconsin Model (Fish Bioenergetics 3.0, Hanson et al. 1997), configured for age-0 Arctic grayling (Table 4-1). Model inputs were average daily temperatures from swim-up to 23 August and the respective mean mass of the YOY grayling on these sampling dates.

In my bioenergetic simulations I first adjusted food consumption (P-value) to meet the observed final mass observed in each stream using their respective temperature regimes. I then determined what the final mass for a YOY grayling would be if I substituted the temperature regime in the artificial stream for that observed in the natural stream. Secondly, I asked what the final mass would be if I substituted the P-value observed in the artificial stream for that observed in the natural stream? I estimated the effect of temperature on the growth (Growth $_T$), as

$$\text{Growth}_T = \left[\frac{|OBS_{ART} - PRE_{Part\&Tnat}|}{OBS_{NAT} - OBS_{ART}} \right] \times 100\%$$

where OBS_{NAT} and OBS_{ART} are the observed mass of YOY grayling on 23 August in the natural and artificial stream, respectively, and $PRE_{Part\&Tnat}$ is the predicted mass of grayling based on the P-value from the artificial stream and the temperature regime from the natural stream. I estimated the effect of food availability on the growth (Growth_F), as

$$\text{Growth}_F = \left[\frac{|OBS_{ART} - PRE_{Pnat\&Tart}|}{OBS_{NAT} - OBS_{ART}} \right] \times 100\%$$

where OBS_{NAT} and OBS_{ART} are the observed mass of YOY grayling on 23 August, in the natural and artificial stream, respectively, and $PRE_{Pnat\&Tart}$ is the estimated mass of grayling based on the P-value from the natural stream and the temperature regime from the artificial stream. My ability to determine the influence of temperature is imperfect in that there is an indirect affect of temperature on C_{max}, the maximum specific feeding rate. However, for the purposes of this study, this indirect effect of temperature is likely small, particularly over the relatively short simulation times used in this study. I also conducted sensitivity analyses for the P-value and activity multiplier by changing these inputs by 25%, 50%, and 100%.

Statistical analyses

I employed one-sample hypotheses testing (OSH; Sokal and Rohlf 1995), using data from general and benthic stream surveys (e.g., substrate, cover, water chemistry, epilithon, CPOM, benthic invertebrates), for comparisons between the artificial and natural streams. My interest was in comparing the average value of a measured variable from the artificial stream to the distribution of values among natural streams. When the number of natural streams sampled was limited, I used general linear modeling (GLM) followed by Tukey's multiple comparison tests for comparisons between the artificial and reference streams (e.g., fish, invertebrate drift, head capsule size). Analysis of covariance (ANCOVA) was used to determine if YOY were of different condition (mass-at-length) among streams and years; mass-length data were square root transformed. I used the Kolmogorov-Smirnov test to examine data for normality and Levene median test for homogeneity of variances. For all statistical tests, I used $\alpha = 0.05$ as a critical level of significance (after performing the Bonferroni adjustment, when required to reduce the experimentwise error rate).

Results

Physicochemical

Large-scale differences in habitat between the artificial and reference streams include mesohabitat composition and the number of side channels. Although natural streams that drain areas of fine sediment tend to have single, well-defined channels, most natural streams in the Barrenlands are multi-channelled, with some streams having over six side channels. In contrast, the artificial stream was constrained by steep (10 - 90°) and high (2 - 10 m) banks, with a single channel throughout its entire length. Natural streams

typically contain a diversity of mesohabitat types. Despite its length (3.4 km), however, the artificial stream has a limited number of habitat types, with wetland and boulder garden absent. In addition, the proportions of the habitat types differ from these found in reference streams. For example, natural streams had more riffles (33% vs. 4%) and pools (11% vs. 1%), whereas, the artificial stream had more cascades (7% vs. 1%) and flats (55% vs. 18%) (OSH; $df = 19$, $p < 0.05$). Cover for YOY grayling in reference streams was nearly double that found in the artificial stream (Table 4-2). In addition, the cover types available to grayling were more diverse in the natural streams than the artificial, where vegetation (aquatic and terrestrial) was almost entirely absent (Table 4-2).

Substrate sizes in the artificial stream were significantly smaller than those found in the reference streams. Fine substrates (silt, clay, and sand) dominated 44% of the substrate composition in the artificial stream while in the natural streams, fines comprised only 14%; the proportion of sand was significantly greater in the artificial stream (OSH; $df = 19$, $p < 0.05$). Moreover, boulders comprised only 16% of the substrate in the artificial stream but 56% in natural streams (OSH; $df = 19$, $p < 0.05$). .

Water chemistry in the artificial stream was similar to that found in natural streams. Total phosphorus in the artificial was not significantly different from that measured in natural stream systems (9.85 $\mu g \cdot L^{-1}$ and 6.92 $\mu g \cdot L^{-1}$ $\pm$ 0.72 standard error (SE), respectively, OSH; $df = 5$, $p < 0.05$). However, total nitrogen was higher in the artificial stream than in the natural streams (321.56 $\mu g \cdot L^{-1}$ and 167.20 $\mu g \cdot L^{-1}$ $\pm$ 26.7 SE; OSH; $df = 5$, $p < 0.05$). At times, particularly during high flow events (spring and fall), turbidity and suspended solids levels would briefly but dramatically increase in the artificial stream (N.E. Jones, personal observation).

Natural streams accumulated a mean of 851 degree-days from swim-up of YOY Arctic grayling to 31 August (Table 4-3). Daily water temperatures in the artificial stream averaged 0.9 °C colder than in the natural streams during the growth period (Table 4-3). This seemingly small difference accumulated to an average deficit of 56 degree-days from swim-up to out-migration in late August.

Biological

Vegetation and Organic Matter

A major difference between the artificial and reference streams is in the amount of living and dead plant material in the stream channels and adjacent riparian areas. The riparian zone of natural Barrenland streams are generally well vegetated. In well-drained riparian zones dwarf heath and scattered low shrub tundra dominate, whereas sedge tussock is common in poorly drained areas. In contrast, the riparian zone of the artificial stream is dominated by a thick layer of blast rock, although, willow plugs have been planted to stabilize banks in a few areas. Grasses covered 44 ± 5% SE of the ground in natural riparian zones, but only 4% in the artificial (OSH; $df = 8$, $p < 0.05$). Similarly, cover by shrubs averaged 58 ± 5% SE in natural riparian zones, but only 1% in the artificial stream (OSH; $df = 8$, $p < 0.05$). The average density of shrub stems within 1 m of the stream was 0.86 m^{-2} ± 0.12 SE and 0.06 m^{-2} in the reference and artificial streams, respectively (OSH; $df = 8$, $p < 0.05$).

Aquatic plants, consisting of macrophytes, algae, and bryophytes, were generally abundant in natural streams but were rare in the artificial and those that existed in the latter were mostly planted. Epilithon abundance, particularly *Zygnema* spp., was significantly greater in the natural streams compared to the artificial stream (OSH, $p <$

0.05, Fig. 4-2a). Depositional areas of fine substrate organic matter in natural streams also supported an abundance of aquatic macrophytes (e.g., bur-reed, *Sparganium hyperboreum* and mare's-tail, *Hippuris vulgaris*), covering 17 ± 5% SE of the stream bed by mid-July. Macrophytes in the artificial stream consisted of planted Arctic pendant grass, *Arctophila fulva*, which thinly covered only 1% of the streambed. Bryophytes were common in some natural streams, covering 10 ± 3% SE of the stream bed, but were absent from the artificial stream.

Stemming from a lack of riparian vegetation, the artificial stream contained approximately one-tenth the coarse particulate organic matter (CPOM) found in the natural streams (OSH, $p < 0.05$, Fig. 4-2b). In the natural streams, many sections of riffle pass through thick growths of dwarf birch and willow, which contribute relatively small pieces of woody debris (mean length and diameter: 370 mm and 5 mm, respectively) to the channel. Woody debris volume in the artificial stream, 215 $cm^3 \cdot 100m^{-2}$ of stream bed, was about 4-fold lower than that in the natural streams, 917 ± 350 $cm^3 \cdot 100m^{-2}$ mean ± SE. Essentially all the woody debris in the artificial stream were willow plugs added as remediation during 1998 - 2000.

Invertebrates

Although there was considerable variation among streams and years, higher numbers of benthic invertebrates were generally contained in the natural streams than artificial stream, especially in riffles (OSH, $p < 0.05$, Fig. 4-2c). Differences were even greater for benthic invertebrate biomass estimates (OSH, $p < 0.05$, Fig. 4-2d), suggesting that the benthic invertebrates in the natural streams were larger. Dipterans were well represented

in all streams, contributing about 45% of all individuals and 62% by mass, 19% of which were chironomids.

Numbers of small invertebrates (e.g., microcrustaceans, including cladocerans, copepods, and ostracods) in the drift did not differ between the artificial and natural streams (GLM, n = 18 per date and stream, $p > 0.05$, Fig. 4-3a). However, there were significantly fewer large organisms (e.g., insect larvae, including chironomids, simuliids, ephemeropterans) in the drift of the artificial stream on all sampling dates compared to natural streams (GLM, Fig. 4-3b). Mean drift biomass in the artificial and natural streams were similar in 1999. In 2000, however, drift biomass in natural streams was typically higher (GLM, Fig. 4-3c). As suggested above, the head capsule widths of drifting larval Chironomidae were larger in the natural streams (Polar-Vulture and Pigeon) than in the artificial stream (GLM, df = 223, $p < 0.05$), however, size of larval Simuliidae was similar among streams (GLM, df = 252, $p = 0.06$).

Fish

Spawning surveys and radio telemetry studies indicated that adult and juvenile Arctic grayling were able to migrate successfully through the artificial stream and its three culverts (N.E. Jones, unpublished data). Other species and age-classes, including slimy sculpin and burbot, were unable to ascend a second culvert, 700 m upstream from Kodiak Lake (Fig. 4-1). Depending on the year, between 200 and 300 grayling were observed migrating into the artificial stream. Although a quantitative estimate of spawning success was not determined, YOY grayling were produced in relatively large numbers, particularly in the lower end of the stream where the majority of spawning occurred (N.E. Jones, unpublished data).

Fish communities: density and biomass

Fish community composition in the artificial stream was similar to that in the intensively fished natural stream, Polar-Vulture. Age-0 grayling dominated both communities, numerically and by biomass. Other species in both streams included slimy sculpin and burbot. Total densities of fish in the artificial stream were similar to (1998) or less than (1999, 2000) densities found in Polar-Vulture (GLM, $df = 55$, $p < 0.05$, Fig. 4-4a). In contrast, fish biomass was consistently and significantly greater in Polar-Vulture on all dates (GLM, $df = 55$, $p < 0.05$; Fig. 4-4b). Similarly, grayling biomass was generally greater in Polar-Vulture (GLM, $df = 55$, $p < 0.05$; Fig. 4-4c).

Growth and production of age-0 grayling

Growth varied considerably among years, related to differences in temperature, discharge, and invertebrate densities (Table 4-4). The two most intensively studied reference streams, Polar-Vulture and Pigeon, produced the slowest and fastest growing YOY grayling, respectively, among natural streams. By 23 August, prior to out-migration, YOY in natural streams averaged 2.74 g ± 0.44 SE, whereas YOY in the artificial stream were only 1.18 g ± 0.14 SE (Table 4-5). Differences in growth between the artificial and natural streams became more prominent over the course of a summer (Fig. 4-5a). Analysis of covariance indicated a significant interaction ($p = 0.003$) between the covariate (length) and the independent factor (stream), indicating that the growth rates differed between the artificial and natural streams (Fig. 4-5a). There appears to be little difference in condition (i.e., mass at length) among streams and years (Fig. 4-5b). Hence, YOY from different streams followed similar allometries, but not at the same rate. The large difference in growth, in concert with estimates of YOY grayling

density, meant that standing crop in the artificial stream averaged 37% of that found in Polar-Vulture (Fig. 4-4c).

Diet analyses

The composition of invertebrates in the diets of YOY grayling was stream dependent. Grayling stomachs from the artificial stream and Polar-Vulture contained a very similar composition of invertebrates, roughly 75% chironomids and 10% simuliids, whereas fish from Pigeon contained 33% chironomids and 46% simuliids. The head capsule widths of Chironomidae (GLM, $df = 333$, $p < 0.05$) and Simuliidae (GLM, $df = 304$, $p < 0.05$) in the diets were larger on 50% of sampling dates in the natural streams (Polar-Vulture and Pigeon) versus the artificial.

Bioenergetic simulations

My simulations estimated that 11% of the difference in the mass of YOY grayling between the artificial and natural streams can be attributed to the cooler temperature of the artificial stream, whereas 80% can be attributed to reduced food consumption. The relative importance of temperature varied by year (Table 4-6). During cooler summers (e.g., 1999), temperature had more of an influence on growth, but during warm summers (e.g., 2000), temperature had little bearing on differences in growth (Table 4-6).

My sensitivity analysis of the bioenergetics model indicated that a 50% increase in the P-value resulted in a 4-fold increase in body mass, and a 100% increase resulted in a 13-fold increase in body mass, and thus food consumption could contribute to the observed differences in growth between the artificial and natural streams. The bioenergetics model was less sensitive to changes in the activity multiplier. A 50%

increase in activity resulted in approximately a 2-fold reduction in body mass, and a 100% increase resulted in a 7-fold reduction in body mass.

Discussion

Assessing the artificial stream as productive fish habitat

My assessment of the artificial stream is based on a hierarchical framework of stream functions focused on the production of YOY Arctic grayling: can grayling successfully migrate through the channel, do the grayling spawn in the channel, do the eggs hatch, and do the young grayling grow to a sufficient size? Each function is needed if the artificial stream is to compensate for lost habitat and result in no-net-loss of productive capacity. Reference streams provided standards and therefore enabled us to measure effectiveness. The artificial stream met or approached expectations for some of these functions. Although not quantified in this study, I observed that watershed connectivity was at least partially restored and this allowed adult grayling and lake trout to migrate throughout the drainage basin, i.e., the artificial stream restored landscape-scale habitat use (N. E. Jones, unpublished data). Because Barrenlands grayling, with their adfluvial life history, migrate among the chains of lakes and streams in the watershed, its fragmentation would mean the loss of habitat availability at this scale, which could have significant population-level consequences (Kentaro and Shoichiro 2002). As such, restoring watershed connectivity was paramount in the development of the artificial stream. Efforts by BHP-B to maintain a bi-directional fish weir were beset with technical difficulties, however, I estimated that 200 - 300 adult grayling migrated annually into the artificial stream at ice-out. Within the artificial stream, fish passage was needed so that grayling could move to and select among available spawning areas. Although passage

throughout the artificial stream was achieved for adult grayling and lake trout, slimy sculpin and burbot appeared unable to ascend one of the culverts, suggesting that their populations in the watershed have become fragmented.

A quantitative estimate of spawning success was not determined, but I noted qualitatively that YOY grayling were produced in large numbers, particularly in the lower end of the stream where the majority of spawning occurred (N.E. Jones, unpublished data). Despite these successes, the growth and production of YOY grayling strongly suggests that the quality of nursery habitat is currently deficient in some manner, e.g., food production, physical habitat, or water temperature, and this deficiency is the focus of the subsequent discussion.

Growth of YOY Arctic grayling

Temperature

Water temperature influences the growth of fish both directly, through physiological processes, and indirectly by affecting rates of energy flow and nutrient dynamics. Water temperature in the artificial stream is, on average, 1 °C colder than that observed in natural streams. The cooler temperatures likely result from less direct sunlight reaching the artificial stream due to steep and high stream banks and because the streambed penetrates deep into permafrost. In contrast, natural Barrenland streams flow through wide shallow valleys and tend to spread laterally. Thus, even with the low angle of incidence of sunlight characteristic of high latitudes, natural streams are almost always well lit throughout the long summer days of the Arctic.

My bioenergetics simulations nevertheless suggest that summer water temperatures had little influence on the differences in growth. On average, only 11% of the difference

in the mass of YOY grayling can be attributed to the cooler temperature of the artificial stream. Other factors, namely food availability and possibly physical habitat, are clearly more important than temperature. Similarly, summer growth of rainbow trout (*Oncorhynchus mykiss*) in the Sierre Nevadas was not directly related to temperature (Railsback and Rose 1999). Although the growth of YOY salmonids in streams can be affected by temperature, particularly when it affects emergence times and thus the length of the growing season (Holtby 1988), emergence in the artificial stream was unaffected.

Nutrients and energy resources

In contrast to the limited effect of temperature, bioenergetic simulations indicated that differences in food consumption could explain about 80% of the difference in growth of YOY grayling between the artificial and natural streams, suggesting, that food availability differed. The well vegetated banks of natural streams contrast sharply to the waste rock used to line the channel and riparian zone of the artificial stream. Although concentrations of commonly limiting nutrients (phosphorus and nitrogen) in the artificial stream are similar to or greater than those measured in natural streams, the waste rock in the artificial stream supports little algal growth. The artificial stream also lacks the large amounts of aquatic macrophytes found in natural streams. It seems likely that this paucity of sources of allochthonous and autochthonous organic matter is ultimately a major contributor to the reduced growth and production of YOY grayling in the artificial stream. Moreover, it is likely that the habitat needed by terrestrial and aquatic plants is not currently available and that successional processes are required for their persistence, even if they would be manually introduced. In addition, high flows in the spring and fall

result in heavy scour and erosion, further hampering plant colonization and growth (Waters 1995).

In turn, the lack of terrestrial and aquatic plant growth leads to low amounts of particulate organic matter and woody debris. Unlike alluvial streams, where channel migration plays an important role in woody debris recruitment, stream channels in Barrenland streams are generally stable, permafrost-bound, and boulder-dominated colluvial systems, i.e., fluvial process are relatively ineffective at removing material deposited on the valley floor. Natural process that recruit CPOM and woody debris in natural Barrenland streams include fluvial transport of floodplain organic matter, leaf fall, and Barrenland caribou (*Rangifer tarandus)* that when migrating across the streams trample the riparian shrubs and kick pieces into the stream (Chapter II). However, the floodplain, and its crossing by caribou, in the artificial stream is extremely limited due to its deeply incised channel design.

The importance of plants and organic matter as food and substrate for stream invertebrates is well known (Egglishaw 1964; Reice 1980, Flory and Milner 1999). The density and biomass of benthic invertebrates were much reduced in the artificial stream, leading to low drift densities of macroinvertebrates. In addition, the head capsules of chironomids were often smaller in the artificial stream, suggesting food limitation at this trophic level. Successful colonization and growth of invertebrates will also depend on the development of suitable habitat; unassisted, this process will likely require many years before the benthic invertebrate community resembles that in natural streams (Milner et al. 2000). Also, heavy sediment pulses and bed scouring likely damage

invertebrate assemblages and hamper invertebrate establishment and growth (Waters 1995; Shaw and Richardson 2001).

Young-of-the-year Arctic grayling in natural Barrenland streams selected aquatic insect larvae, particularly chironomids and simuliids, as primary prey whereas smaller microcrustacea, nematodes, and mites were strongly avoided (Chapter III). Further, the sizes of chironomids and simuliids in the stomachs of grayling were frequently larger than those available in the drift, indicating a strong size-based foraging strategy. These forage preferences, and the reduced numbers of large-sized prey available in the drift of the artificial stream, support the hypothesis that the forage base for grayling is limiting their growth in the artificial stream.

Annual Variability in Temperature and Production

Invertebrate drift and benthic invertebrate density and biomass varied considerably among the four study years in relation to air and water temperature, rainfall, and discharge. Correspondingly, YOY grayling were larger in the warm, dry year (1998) when food (i.e., macroinvertebrates) was plentiful. Conversely, epilithon abundance was low, perhaps because of high invertebrate numbers. The opposite pattern was observed in the cool, wet year (1999). These relationships are consistent with those observed recently among discharge, water temperature, and growth of YOY grayling in Alaska (Deegan et al. 1999). The importance of climate in relation to stream productivity and fish growth is evident from the strong relationship between growing degree-days and end-of-season fish mass in Polar-Vulture stream (Fig. 4-6). The strength of the relationship suggests that fish growth is affected more by climatic factors controlling annual productivity than by the direct effects of temperature on fish physiology. In the

artificial stream, however, the relationship between grayling growth and climate is greatly muted. I suggest that food limitation, based ultimately on a paucity of organic matter and suitable habitat for invertebrates, masks the influence of climate in the artificial stream, i.e., the system is unable to respond to the more favourable conditions of a warm, dry year by producing larger YOY fish.

Physical Habitat

Relative to the reference streams, habitat complexity at small and large-scales was considerably reduced in the artificial stream. The artificial stream had only one fairly straight channel and was deficient in or lacked several mesohabitat types, comparable to many perturbed rivers that have lost channel structure, complex banks, and important snag habitat (Sedell and Froggatt 1984; Benke et al. 1985; Mitro and Zale 2002). At small-scales, the artificial stream lacked large substrates, woody debris, and aquatic and terrestrial vegetation, which can create hydraulically complex flows, including flow refuges, that provide habitat for YOY grayling, invertebrates, and other aquatic life. Large substrates also provide a stable surface area and interstitial space for invertebrates relative to small substrates; as such, they frequently harbour greater numbers and biomass, and a diversity of benthic invertebrates (e.g., McElhone and Davies 1983). The effects of fine sediment on invertebrate production can be dramatic and can cascade to higher trophic levels. For example, the introduction of sand into Hunt Creek, Michigan resulted in stream aggradation, the replacement of pool and riffles series with continuous run habitat, a large reduction in food for brook trout (*Salvelinus fontinalis*), and a 50% reduction in their numbers (Alexander and Hansen 1986).

Complex habitats often support greater standing crops and production (e.g., Murphy et al. 1984; McMahon and Hartman 1989; Fausch and Northcote 1992) and enhance the growth and survival of stream dwelling fishes (e.g., Quinn and Peterson 1996; Sundbaum and Näslund 1998). Observational studies indicate that salmonids seek optimal conditions of depth and velocity for foraging, within the constraints of competition (Fausch 1984) and predation (Lima and Dill 1990). Experimental evidence (Fausch 1993, and references therein) suggests that habitat structures provide three main features related to the trade-offs between foraging and predation risk: (i) velocity refuge, (ii) visual isolation, and (iii) overhead cover. Structures that provide visual isolation from other fish reduce energetically costly agonistic behaviour (Sundbaum and Näslund 1998), and overhead cover such as riparian vegetation can reduce the degree of predator vigilance. Physical habitats that provide velocity refuge, such as boulders, allow fish to hold low velocity positions adjacent to faster water currents and thus maximize their energy intake from drifting food items while minimizing the cost of swimming to maintain position (Fausch and White 1981; Fausch 1984; McLaughlin and Noakes 1998). Interestingly, the size and composition of invertebrates in the diets of YOY grayling in the natural and artificial streams reveal little if any difference, despite poor growth in the artificial stream. This similarity of stomach contents contrasts with the differences in the invertebrate prey base and suggests that grayling in the artificial stream may have to expend more energy in obtaining their food requirements, ultimately resulting in a lower net gain in energy and poor growth. Sensitivity analyses of the bioenergetics model indicated that a 50% increase in the activity multiplier resulted in a 2-fold reduction in body mass, and suggest that increased swimming costs could contribute to the observed

differences in growth between the artificial and natural streams. Still, the model was almost twice as sensitive to changes in food consumption (P-value).

Perspective

The compensation of habitat in the artificial stream has been neither a success nor a failure, instead there has been a progression of successes necessary for compensation. In this hierarchical framework, the artificial stream allows grayling to migrate through and spawn in it and the eggs to hatch; however, as nursery habitat it offers cooler temperatures, low invertebrate production, and physically simple habitat, and as a result produces relatively small YOY, even though fish densities in the artificial stream are lower than those observed in natural streams. Temperature effects appear limited, and although habitat complexity may have an influence on the overall productivity, it is doubtful that grayling growth would achieve the levels observed in reference streams if complexity alone were increased in the artificial stream. Rather, I suggest that the scarcity of organic matter in the artificial stream is primarily limiting the overall growth and productivity of benthic invertebrates, ultimately leading to poor growth and production of YOY Arctic grayling. Importantly, DFO's (1986, p. 28) definition of productive capacity explicitly acknowledges the importance of food and trophic interactions. This differs from many traditional stream habitat management plans, in which managers typically focus on modification of the physical structure of streams via instream habitat structures, without much consideration of the flow of energy and nutrients. I strongly urge habitat managers to use all available knowledge to design compensation programs, not just a physical perspective. Some of the problems

associated with the artificial stream certainly could have been predicted from an understanding of stream ecosystem ecology.

The growth of young fish can have significant implications at the population level, and thus directly affect the productive capacity of an ecosystem (Holtby 1988). Size-dependent mortality, stemming from overwinter starvation (Post and Evans 1989) and predation (Post et al. 1999), is frequently observed in cohorts of young fish (Miller et al. 1988; Post and Parkinson 2001). For young fish, the chances of an individual surviving a period of low food availability, such as the long arctic winter, is largely based on their energy reserves and the rate at which they are used metabolically. It is thus reasonable to suggest that age-0 grayling in the artificial stream, which have reached an end-of-summer mass approximately half that observed in natural streams, may experience reduced survival during their first winter. In turn, recruitment into the breeding population may be impaired.

As a result of my assessment of fish production and the productive capacity of the artificial stream, managers can begin to make defensible decisions and guide the subsequent work that will be required for compensation. The objectives of future studies will need to consider a number of important questions, such as (i) what can be done to improve the growth of grayling as we continue to learn about the relative roles of food production, physical habitat, and temperature? (ii) at what point will grayling have reached an acceptable rate of growth? (iii) because the artificial stream is a completely new ecosystem and ecological succession in the Arctic is slow, how can we speed-up the successional process? And (iv) how long should compensation take? These questions are challenging, but the characteristics of this ecosystem and the information that my studies

have provided offer an unparalleled opportunity to advance the study of fish habitat compensation and stream restoration ecology.

Literature Cited

Alexander, G.R., and Hansen, E.A. 1986. Sand bed load in a brook trout, *Salvelinus fontinalis*, stream. N. Am. J. Fish. Manag. 6: 9-23.

Benke, A.C., Henry, R.L. III, Gillepsie, D.M., and Hunter. R.J. 1985. Importance of snag habitat for animal production in southeastern streams. Fisheries, 10:8-13.

Bradshaw, A.D. 1996. Underlying principles of restoration. Can. J. Fish. Aquat. Sci. 53(Suppl. 1): 3-9.

Deegan, L.A., Golden, H.E., Harvey, C.J., and Peterson, B.J. 1999. Influence of environmental variability on the growth of age-0 and adult Arctic grayling. Trans. Amer. Fish. Soc. 128: 1163-1175.

Department of Fisheries and Oceans (DFO). 1986. The Department of Fisheries and Oceans policy for the management of fish habitat. Communications Directorate, Fisheries and Oceans Canada, Ottawa, Ontario.

Egglishaw, H.J. 1964. The distributional relationship between the bottom fauna and plant detritus in streams. J. Anim. Ecol. 33: 463-476.

Environment Canada. 1991. Canadian climate normals 1961-1990. Ottawa. http://www.msc-smc.ec.gc.ca/climate/climate_normals/index_e.cfm

Fausch, K.D. 1984. Profitable stream positions for salmonids: relating specific growth rate to net energy gain. Can. J. Fish. Aquat. Sci. 62: 441-451.

Fausch, K.D. 1993. Experimental analysis of microhabitat selection by juvenile steelhead (*Oncorhynchus mykiss*) and coho salmon (*O. kisutch*) in a British Columbia stream. Can. J. Fish. Aquat. Sci. 50: 1198-1207.

Fausch, K.D., and Northcote, T.G. 1992. Large woody debris and salmonid habitat in a coastal British Columbia stream. Can. J. Fish. Aquat. Sci. 49: 682-693.

Fausch, K.D., and White, R.J. 1981. Competition between brook trout (*Salvelinus fontinalis*) and brown trout (*Salmo trutta*) for positions in a Michigan stream. Can. J. Fish. Aquat. Sci. 38: 1220-1227.

Flory, E.A. and Milner, A.M. 1999. Influence of riparian vegetation on invertebrate assemblages in a recently formed stream in Glacier Bay National Park, Alaska. J. N. Am. Benthol. Soc. 18: 261-273.

Harrison, J. 1995. Young-of-the-year Arctic grayling (*Thymallus arcticus*) metabolism: scaling with size, temperature and flow. Senior honours thesis, Brown University. pp: 31. Brown University, Providence, RI 02912 USA.

Hanson, P.T., Johnson, T., Kitchell, J., and Schindler, D. E. 1997. Fish bioenergetics 3.0. University of Wisconsin Sea Grant Institute, Report WISCU-T-97-001, Madison, Wisconsin.

Holtby, L.B. 1988. Effects of logging on stream temperatures in Carnation Creek, British Columbia, and associated impacts on the coho salmon (*Oncorhynchus kisutch*). Can. J. Fish. Aquat. Sci. 45: 502-515.

Kentaro, M. and Shoichiro, Y. 2002. Effects of habitat fragmentation by damming on the persistence of stream-dwelling charr populations. Conserv. Bio. 16: 1318-1323.

Kitchell, J.F., Stewart, D.J., Weininger, D. 1977. Applications of a bioenergetics model to yellow perch (*Perca flavescens*) and walleye (*Stizostedion vitreum vitreum*). J. Fish. Res. Board Can. 34: 1922-1935.

Lima, S.L., and Dill, L.M. 1990. Behavioural decisions made under the risk of predation: a review and prospectus. Can. J. Zool. 68: 619-640.

McElhone, M.J., and Davies, R.W. 1983. The influence of rock surface area on the microdistribution and sampling of attached riffle-dwelling Trichoptera in Hartley Creek, Alberta, Canada. Can. J. Zool. 61: 2300-2304.

McLaughlin, R.L., and. Noakes, D.L.G. 1998. Going against the flow: an examination of the propulsive movements made by young brook trout in streams. Can. J. Fish. Aquat. Sci. 55: 853-860.

McMahon, T.E., and Hartman, G.R. 1989. Influence of cover complexity and current velocity on winter habitat use by juvenile coho salmon (*Oncorhynchus kisutch*). Can. J. Fish. Aquat. Sci. 46: 1551-1557

Miller, T.J., L.B. Crowder, J.A. Rice and E.A. Marshall. 1988. Larval size and recruitment mechanisms in fishes: toward a conceptual framework. Can. J. Fish. Aquat. Sci. 45: 1678-1670.

Milner, A.M., Knudsen, E., Soiseth, C., Robertson, A.L., Schell, D., Phillips, I.T., and Magnusson, K. 2000. Colonization and development of stream across a 200 year gradient in Glacier Bay National Park, Alaska, USA. Can. J. Fish. Aquat. Sci. 57: 2319-2335.

Minns, C.K. 1997. Quantifying "no net loss" of productivity of fish habitats. Can. J. Fish. Aquat. Sci. 54: 2463-2473.

Minns, C.K., Kelso, J.R.M., and Randall, R.G. 1996. Detecting the response of fish to habitat alterations in freshwater systems. Can. J. Fish. Aquat. Sci. 53(Suppl. 1): 403-414.

Mitro, M.G., and Zale, A.V. 2002. Seasonal survival, movements, and habitat use of age-0 rainbow trout in the Henrys Fork of the Snake River. Trans. Amer. Fish. Soc. 131: 271-286.

Murphy, M.L., Koski, K.V., Heifetz, J., Johnson, S.W., Kirchhofer, D., and Thedinga, J.F. 1984. Role of large organic debris as winter habitat for juvenile salmonids in Alaska streams. Proceedings of the Annual Conference Western Association of Fish and Wildlife Agencies 64: 251-262.

Ontario Ministry of Natural Resources (OMNR). 1987. Manual of instructions: aquatic habitat surveys. Eighth Edition. Ontario Ministry of Natural Resources, Fisheries Branch. Queens Printer for Ontario, Toronto, Ontario.

Post., J.R., and Evans, D.O. 1989. Size-dependent overwinter mortality of young-of-the-year yellow perch (*Perca flavenscens*): laboratory, in situ enclosure, and field experiments. Can. J. Fish Aquat. Sci. 46: 1958-1968

Post, J.R., and Parkinson, E.A. 2001. Energy allocation strategy in age-0 fish: allometry and survival. Ecology 82: 1040-1051.

Post, J.R., Parkinson, E.A., and Johnston, N.T. 1999. Density-dependent processes in structured fish populations: interaction strengths in whole lake experiments. Ecol. Mono. 69: 155-175.

Quinn, T.P., and Peterson, P.N. 1996. The influence of habitat complexity and fish size on over-winter survival and growth of individually marked juvenile coho salmon

(*Oncorhynchus kisutch*) in Big Beef Creek, Washington. Can. J. Fish. Aquat. Sci. 53: 1555-1564.

Railsback, S.F., and Rose, K.A. 1999. Bioenergetics modeling of stream trout growth: temperature and food consumption effects. Trans. Amer. Fish. Soc. 128: 241-256.

Rand, P.S., D.J. Stewart, P.W. Seelbach, M.L. Jones, and L.R. Wedge. 1993. Modeling steelhead population energetics in Lakes Michigan and Ontario. Trans. Am. Fish. Soc. 122: 977-1001.

Reice, S.R. 1980. The role of substratum in benthic macroinvertebrate microdistribution and litter decomposition in a woodland stream Ecology, 61: 580-590.

Ries, R.D., and Perry, S.A. 1995. Potential effects of global climate warming on brook trout growth and prey consumption in central Appalachian streams, USA. Clim. Res. 5: 197-206.

Sedell, J.R. and Froggatt, J.L. 1984. Importance of streamside forests to large rivers: the isolation of the Willamette River, Oregon, U.S.A. from its floodplain by snagging and streamside forest removal, Verh. Internat. Verin. Theor. Ange. Linmol. 22: 1828-34.

Shaw, E.A., and Richardson, J.S. 2001. Direct and indirect effects of sediment pulse duration on stream invertebrate assemblages and rainbow trout (*Oncorhynchus mykiss*) growth and survival. Can. J. Fish. Aquat. Sci. 58: 2213-2221.

Sokal, R.R., and Rohlf, F.J. 1995. Biometry: The Principles and Practice of Statistics in Biological Research. W.H. Freeman and Co., New York, third edition.

Sundbaum, K., and Näslund, I. 1998. Effects of woody debris on the growth and behaviour of brown trout in experimental stream channels. Can. J. Zool. 76: 56-61.

Thornton, K.W., and Lessem, A.S. 1978. A temperature algorithm for modifying biological rates. Trans. Amer. Fish. Soc. 107: 284-287.

Waters, T.F. 1995. Sediment in streams: sources, biological effects, and control. American Fisheries Society. Monograph 7.

Table 4-1. Physiological parameters used in the bioenergetics model for YOY Arctic grayling.

Parameter	Value	Reference
Waste losses (equation 1)[a, b]		
FA - egestion	0.15	Hanson et al. (1997)
UA - excretion	0.1	Hanson et al. (1997)
Respiration (equation 2)[a, c]		
RA – grams of oxygen ($g \cdot g^{-1} \cdot d^{-1}$) consumed by a 1 gram fish at RTO	0.0156	Harrison (1995)
RB - slope of allometric mass function	-0.287	Harrison (1995)
RQ - ($°C^{-1}$) approximates Q_{10}	2.1	Harrison (1995)
RTO - (°C) optimal temperature for respiration	18	Harrison (1995)
RTM - (°C) maximum lethal temperature	26.4	Harrison (1995)
SDA - specific dynamic action	0.172	Hanson et al. (1997)
Activity	1.3	Hanson et al. (1997)
Consumption (equation 3)[a, c]		
CA - intercept of the mass dependence	0.628	Rand et al.(1993)
CB - coefficient of the mass dependence	-0.3	Rand et al.(1993)
CQ - (°C) lower water temperature at which the temperature dependence is a small fraction (CK1) of the maximum consumption rate	5	Rand et al.(1993)
CK1 - small fraction of the maximum	0.33	Rand et al.(1993)

consumption rate		
CTO - (°C) temperature for corresponding to 0.98 of the maximum consumption rate	20	Rand et al.(1993)
CTM - (°C) temperature (≥CTO) at which dependence is still 0.98 of the maximum consumption rate	20	Rand et al.(1993)
CTL - (°C) upper water temperature at which the temperature dependence is a small fraction (CK4) of the maximum consumption rate	24	Rand et al.(1993)
CK4 - small fraction of the maximum consumption rate	0.2	Rand et al.(1993)

[a] Hanson et al. (1997) [b] Kitchell et al. (1977) [c] Thornton and Lessem (1978)

Table 4-2. Mean percentage total cover (± standard error) and its distribution among cover types available to young-of-the-year Arctic grayling in the artificial and two natural streams, Polar-Vulture and Pigeon. Significance (p value) indicate differences between the artificial and natural streams (one sample hypothesis testing). Aquatic and terrestrial vegetation were very scarce in the artificial stream. NA, not applicable.

Stream	Total Cover	Cover types					
		Rock	Depth	Turbulence	Aquatic vegetation	Undercut	Terrestrial vegetation
Artificial	22	39	26	34	0	1	0
Natural	42 (0.3)	24 (3.5)	22 (7.7)	18 (0.0)	22 (3.2)	8 (1.4)	6 (0.3)
Significance	0.009	0.140	0.721	0.001	NA	0.021	NA

Table 4-3. Temperature regime characteristics of the artificial (ART) and natural streams, Polar-Vulture (PV) and Pigeon (PG), from swim-up of young-of-the-year Arctic grayling to 31 August 1998 - 2001. Mean temperature is the overall seasonal average of mean daily temperatures, which are the average of six measurements per day. Mean difference is the difference in mean daily temperatures between natural stream(s) and the artificial stream, averaged over the season. The mean daily temperature in the artificial stream was significantly lower (paired t-tests, $p < 0.05$) in all comparisons with natural streams. Standard errors are in parentheses.

Year	1998		1999		2000			2001	
Swim-up date	19 June		5 July		30 June			6 July	
Number of days	74		57		62			53	
Stream	ART	PV	ART	PV	ART	PV	PG	ART	PV
Mean temperature (°C)	13.3(2.3)	14.0(2.3)	11.0(2.0)	12.0(2.1)	13.5(3.8)	14.6(3.9)	14.1(4.1)	13.3(3.5)	14.2(3.5)
Total degree-days	983	1038	629	685	834	903	877	704	751
Mean difference (°C)		0.7 (0.4)		1.0 (0.3)		1.1 (0.5)	0.7 (0.7)		0.9 (0.0)
Sum of differences (°d)		54.9		56.7		69.4	43.0		47.7

Table 4-4. Annual variation in weather and discharge during June - August, and accumulated degree-days from spawning to 23 August in relation to mean ± standard error epilithon mass, benthic invertebrate density for Polar-Vulture, Pikejaw, and Slipper-Lac de Gras streams, 1998 - 2001. Data on young-of-the-year mean size ± standard error are from Polar-Vulture. For 1998, fish mass on 23 August was estimated based on two prior sampling periods (9 July and 30 July). General linear modelling and multiple comparisons were used to assess differences in biotic characteristics among years. YOY = young-of-the-year.

Characteristics	1998	1999	2000	2001	p value and post hoc tests
Abiotic					
Accumulated rainfall (mm)	88	180	118	134	
Mean discharge ($m^3 \cdot s^{-1}$)	0.03	0.14	0.13	0.16	
Accumulated mean monthly air temperature (°C)	37	28	34	31	
Mean daily water temperature (°C)	13	12	14	14	
Degree-days (°C) from spawning to 23 August	1137	882	1029	934	
Biotic					
Epilithon ($mg \cdot cm^{-2}$)	1.7 (0.7)	2.0 (0.6)	1.9 (0.4)	-	0.94
Benthic density ($ind. \cdot m^{-2}$)	31 480 (7541)	3420 (565)	13 720 (1891)	-	0.023 A B AB
YOY length (mm)	77	57 (0.5)	64 (0.9)	56 (0.47)	< 0.01 A B C B
YOY mass (g)	3.80	1.78 (0.05)	2.55 (0.12)	1.78 (0.04)	< 0.01 A B C B

Table 4-5. Mean mass (g) ± standard error and the absolute and relative difference in mass of young-of-the-year Arctic grayling between the artificial and natural streams on 23 August 1998 – 2001, shortly before out-migration. Number of natural streams studied per year are: 1998 (1), 1999(2), 2000 (9), and 2001(3).

Year	1998[a]	1999	2000	2001	Mean	SE
Artificial	1.60	0.99 (0.02)	1.11 (0.09)	1.01 (0.06)	1.18	0.14
Natural	3.80	2.07 (0.11)	2.91 (0.09)	2.12 (0.2)	2.74	0.44
Difference	-2.20	-1.08	-1.80	-1.11	-1.55	0.27
Relative difference (%)	58	48	38	48	57	2.5

[a] fish mass on 23 August 1998 was estimated based on two prior sampling periods (9 July and 30 July).

Table 4-6. Results of bioenergetics simulations for 1998 – 2001. Relative influence of temperature and food on young-of-the-year Arctic grayling growth as estimated from the simulations. Natural streams are Polar-Vulture (PV) and Pigeon (PG).

Year	1998[a]	1999	2000		2001[b]	
Artificial vs.	PV	PV	PV	PG	PV	Mean
Temperature	13	19	4	2	9	11
Food	81	69	81	93	84	80

[a] mass on 23 August was estimated. See Table 4.

[b] temperatures used in simulations are estimated from those of the artificial stream (artificial stream temperatures plus the mean daily average difference, 0.9 °C).

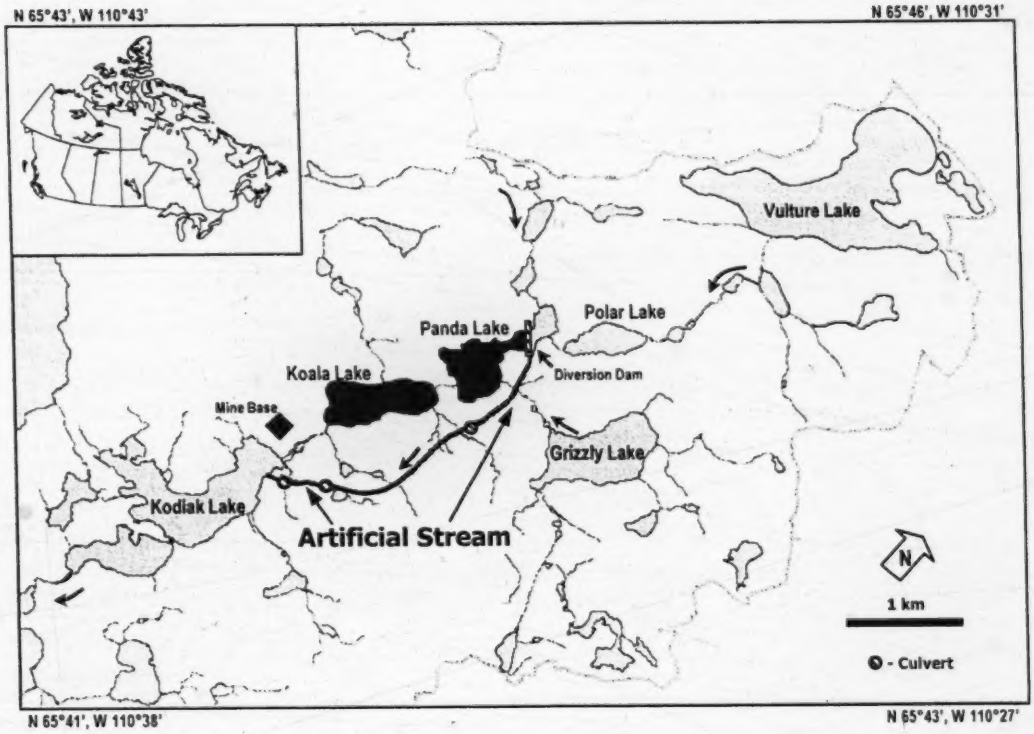

Figure 4-1. Map showing the location of the artificial stream in relation to lakes in the watershed. Koala Lake and the dark portion of Panda Lake were drained and developed as open-pit mines. Water flow, indicated by the arrows, moves from Vulture Lake to Polar Lake through the artificial stream and into Kodiak Lake. Insert: location of study area in the Northwest Territories, Canada.

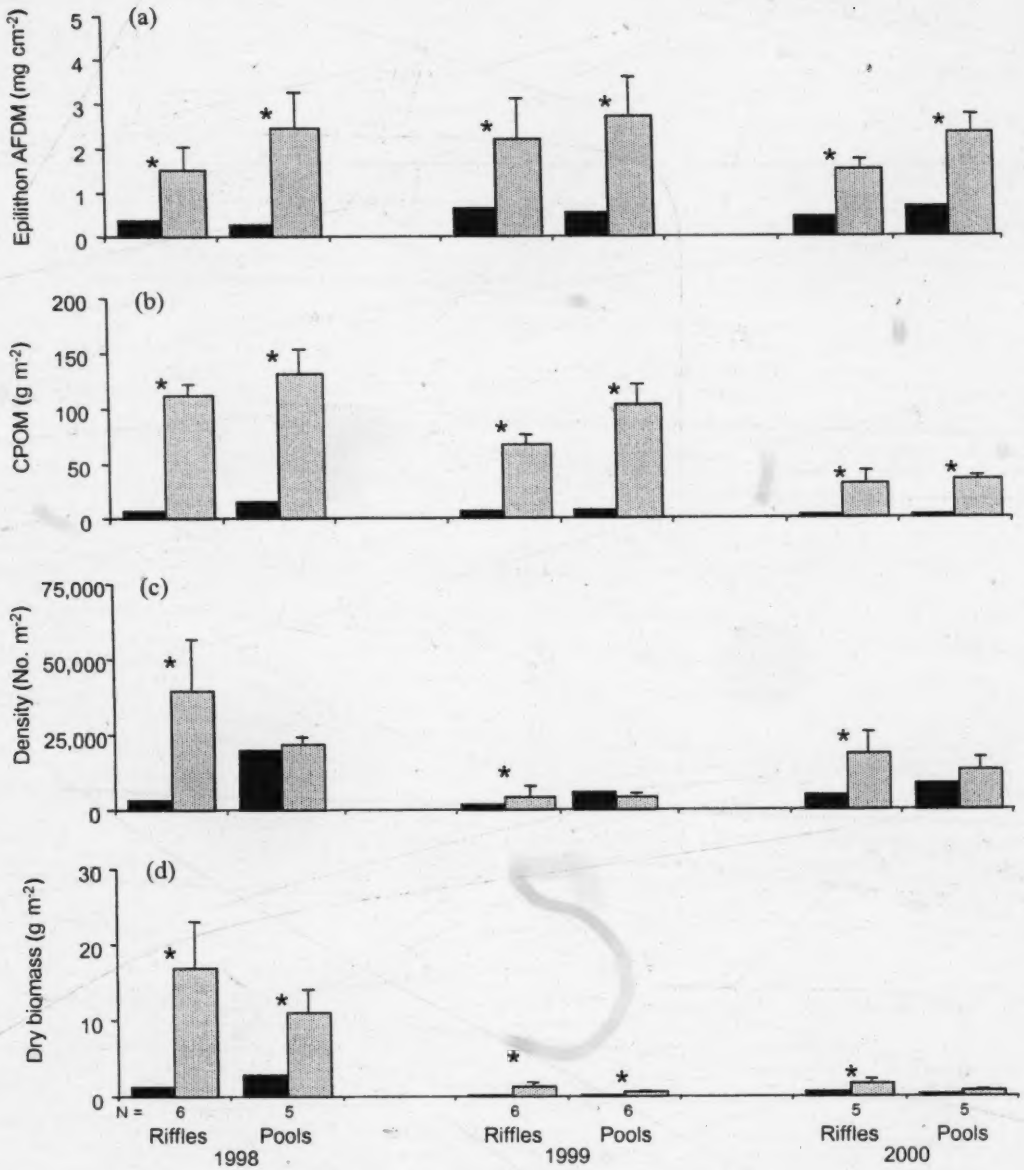

Figure 4-2. Mean (± standard error) amounts of (a) epilithon, and (b) substrate coarse particulate organic matter (CPOM), and benthic invertebrate (c) density and (d) biomass in riffle and pool habitats from the artificial (black) and natural streams (grey), 1998 - 2000. Asterisks indicate significant differences (t-test, $p < 0.05$) between stream types. AFDM = ash-free dry mass.

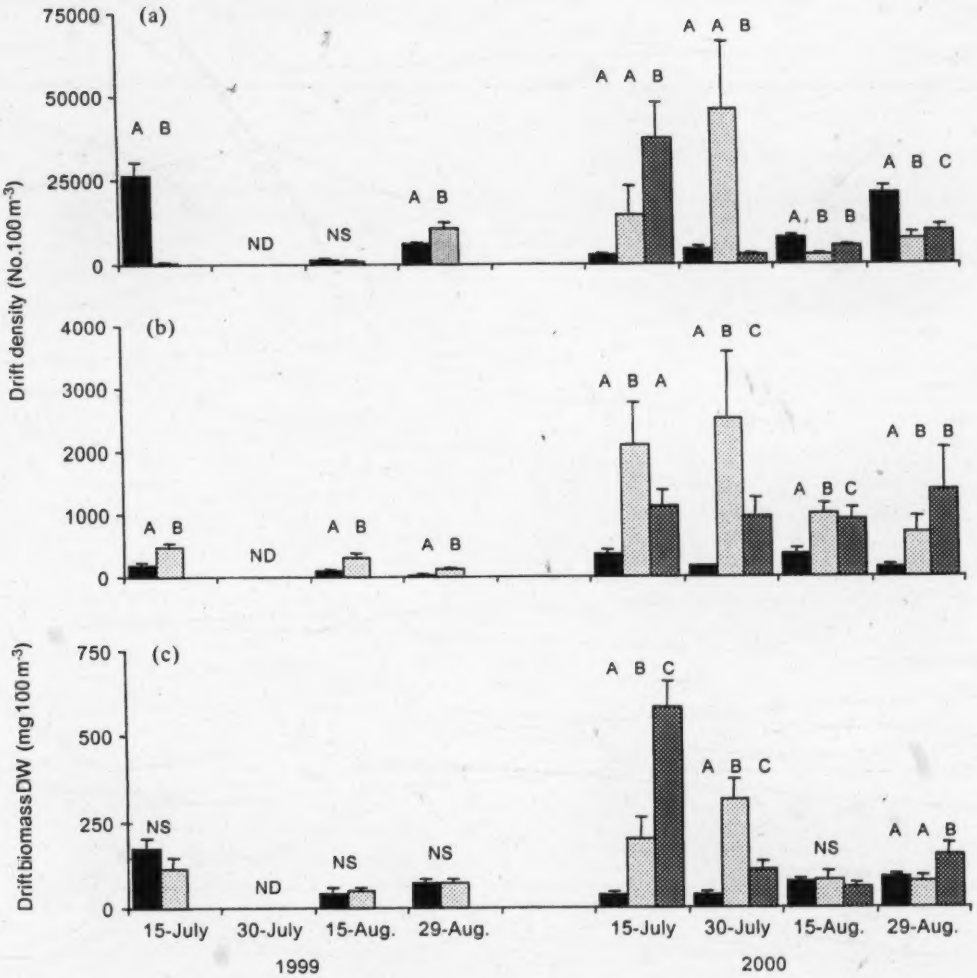

Figure. 4-3. Mean (± standard error) densities in the drift of (a) small (e.g., microcrustaceans) and (b) large (e.g., insects) invertebrates and (c) total drift biomass (dry mass) in the artificial (black) and natural streams, Polar-Vulture (light grey) and Pigeon (dark grey), during four sampling periods 1999 – 2000. Letters indicate significant differences among streams (General linear modeling and multiple comparisons, $p < 0.05$) for each time period; NS = not significant. N = 18 per stream and time period. ND = no data.

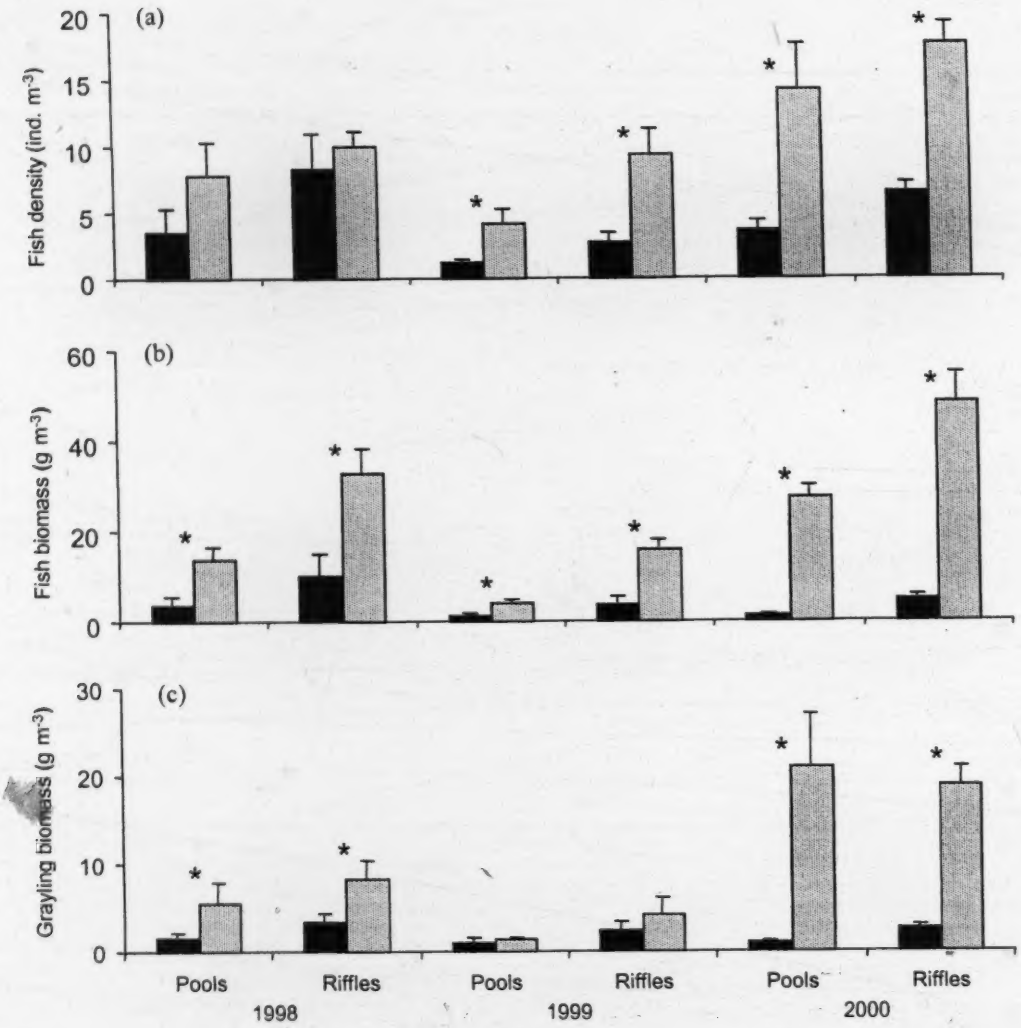

Figure 4-4. Mean (± standard error) (a) density and (b) biomass of all fish and of (c) grayling in pool and riffle habitats in the artificial (black) and Polar-Vulture (grey) streams in 1998 - 2000. Asterisks indicate significant differences (t tests; $p < 0.05$) between streams.

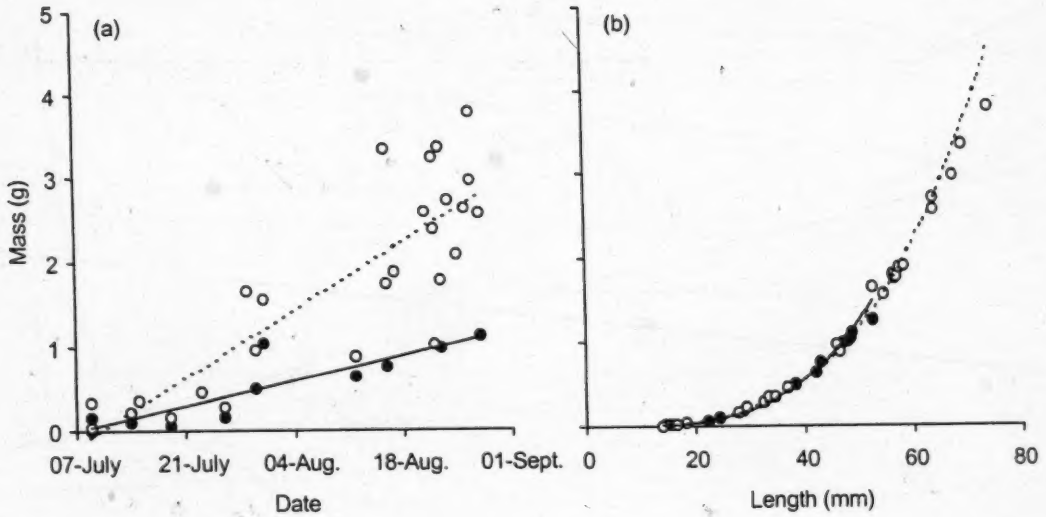

Figure 4-5. The mass of young-of-the-year Arctic grayling (*Thymallus arcticus*) in relation to (a) date and (b) fork length for the artificial (solid circles) and natural streams (open circles). All mass and length data points are means of samples collect during the summers of 1998 - 2001.

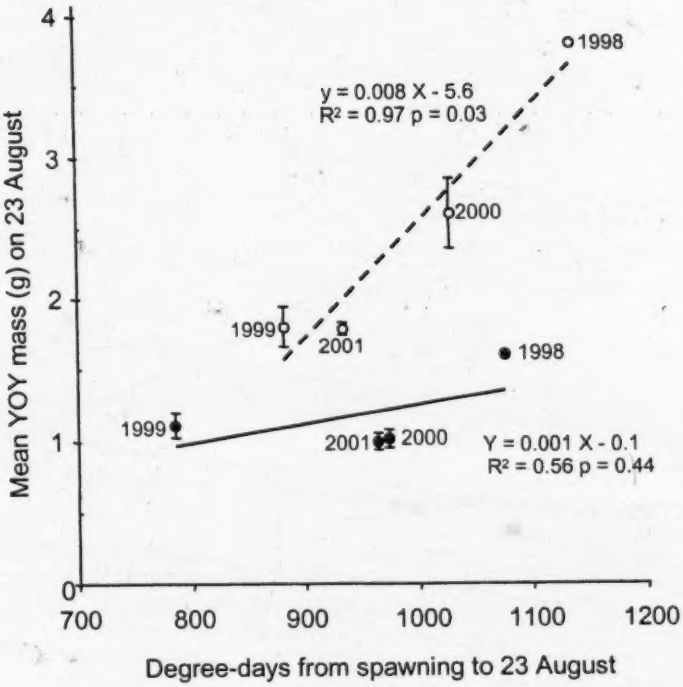

Figure 4-6. Mean mass (± standard error) of young-of-the-year (YOY) Arctic grayling (*Thymallus arcticus*) on 23 August in relation to the number of degree-days (water temperatures above 0 °C) accumulated by the artificial streams (solid line and circles) and Polar-Vulture (dashed line and open circles) streams between the date of spawning by grayling to 23 August. Masses on 23 August 1998 were estimated for both streams from large samples collected on 9 and 30 July 1998. Also indicated are least-squares regression lines and equations.

Chapter V: Resource selection functions for age-0 Arctic grayling (*Thymallus arcticus*) and their application to stream habitat compensation

Introduction

Effective fisheries management requires an understanding of the habitat requirements of aquatic species that potentially are affected by modification of habitat (DFO 1986). For many species or life stages, however, this understanding is poor. Nevertheless, resource managers are often called upon to recommend, design, and implement habitat alterations without the scientific certainty they would prefer (Minns et al. 1996). A poor understanding of the relationship between fish and their habitat is particularly true in arctic regions. However, the need for a better understanding of fish-habitat relations has never been more pressing. In the last 50 years, arctic regions have experienced a steady expansion in both the development of their natural resources and in environmental impacts (Schindler 2001). However, these increasing pressures have not been matched by increases in research directed toward understanding arctic aquatic ecosystems or mitigating ecosystem impacts.

To provide resource managers with the information they require with respect to habitat management, researchers often summarize, in the form of habitat suitability models, patterns of habitat use by animals, to help identify habitats considered as critical or essential (Benaka 1999). From such models, managers can document or predict the availability of those habitats before or after some environmental change has occurred.

Overall, organisms should select habitats that provide the greatest overall gains in survival and reproduction, thus, habitat choice has or is an evolutionary consequence (Boyce and McDonald 1999). For example, at small-scales, some locations in a stream are more energetically profitable for fish than other locations (e.g., Fausch 1984; Hughes and Dill 1990). Thus, determining which habitats are selected more often than others provides fundamental information about how animals meet their requirements for survival.

The development of habitat suitability index (HSI) models, such as those published by the US Fish and Wildlife Service (USFWS 1981), ranges from those based on expert opinion (Delphi technique), to those developed from field data on habitat use and availability. Many HSI models are developed using a combination of approaches, however, methods are rarely tied directly to statistical estimation. For example, the HSI model for riverine Arctic grayling (*Thymallus arcticus*) was developed from the authors' best estimate of habitat suitability in the absence of direct habitat use and availability field data (Hubert et al. 1985). Regardless of their lack of quantitative, empirical, rigor, HSI models can nevertheless provide a basis for improved decision-making and increased understanding because they specify hypotheses of habitat relationships that can be tested and improved. Aside from Hubert et al.'s synthesis, little information exists on Arctic grayling habitat selection (cf. Hughes and Dill 1990).

More recently, fish and wildlife biologists have developed a new set of methods, resource selection functions (RSFs), to describe species-habitat relationships (Boyce and McDonald 1999; Boyce et al. 2002). Similar to HSI models, RSFs are mathematical functions that are proportional to the probability of an area being used by an animal

(Manly et al. 1993). However, RSFs are statistically and quantitatively more rigorous, in that they are always estimated from data (Boyce et al. 2002). In addition, RSFs can simultaneously consider multiple variables, including their interactions, and issues of spatial scale can be explored and modelled, particularly with recent advances in geographic information systems (Boyce and McDonald 1999; Minns et al. 1995).

The main objective of the present study was to determine what habitat characteristics influence the locations chosen by two size-classes of young-of-the-year (YOY) Arctic grayling in an arctic stream through the development of RSFs. Following their development, I validate my grayling RSFs using a withheld sample from the same natural stream, i.e., I test the hypothesis that the probabilities of individual stream locations used by grayling are predictable based on these fish-habitat relationships. I then use the RSFs to assess habitat quality for grayling in a 3.4 km artificial stream constructed as part of a habitat compensation project.

Since 1997, water has been diverted around two lakes, now open-pit diamond mines, through the artificial channel. The objective of the compensation was to restore watershed connectivity for fish migration, and provide spawning and nursery habitats, primarily for Arctic grayling.

Methods

The study was centred in the Barrenlands region of the Northwest Territories, ca. 64°45'N, 110°30'W, roughly 100 km north of the tree-line within the Southern Arctic ecozone. At approximately 450 masl, the streams of this area are the headwaters of the Coppermine, Back, and Burnside rivers, which flow north to the Arctic Ocean. Barrenland streams are generally small (2-50 m wide), and short (80-2900 m) lake-outlet

systems (Chapter II). Freshet begins in late May and flows (0.1 to 7.0 $m^3 \cdot s^{-1}$) continue until late September, when streams freeze completely. Streams can get as warm as 20°C but average ca. 14°C during the summer. Stream water is circumneutral, stained yellow-brown, and low in turbidity (<5 NTU) and conductivity (8-19 $\mu s \cdot cm^{-1}$). Streams are used mainly for spawning and subsequently as nursery habitat for YOY grayling. In September, before the streams freeze, all fish migrate to lakes to over-winter (Chapter II).

Fieldwork was conducted in Polar-Vulture, a natural Barrenlands stream, and in the lower 700 m of the 3.4-km artificial stream, created as part of a habitat compensation agreement (DFO 1986; Table 5-1). Polar-Vulture is a multi-channelled stream containing a diversity of habitats for fish at several spatial scales, whereas the artificial stream consists of a single well-defined channel and rather simple habitat (Fig. 5-1). In the artificial stream, blast rock lines a largely unvegetated riparian zone, whereas, riparian areas of Polar-Vulture are dominated by grasses and shrubs. Aquatic vegetation common in Polar-Vulture (e.g., bur-reed, Sparganium hyperboreum) is also very rare in the artificial stream. In Chapter IV I noted that age-0 grayling dominated the communities in both Polar-Vulture and the artificial stream, both numerically and by biomass. Other species in both streams included slimy sculpin (*Cottus cognatus*) and small numbers of burbot (*Lota lota*). Total densities of fish in Polar-Vulture were greater than densities found in the artificial stream in 1999, the year of this study. Paramount was that YOY grayling in Polar-Vulture were significantly larger (length and mass) than those found in the artificial stream during four years of study (Chapter IV).

Habitat availability

Mesohabitat was classified into cascade, riffle, run, flat, and pool sequences that linearly stratify the streams into discrete units. Microhabitat availability was quantified using stratified random sampling, whereby the number of randomly assigned transects in a mesohabitat type was proportional to the length of the mesohabitat unit. Microhabitat measurements were made along randomly placed transects perpendicular to the axis of the stream. Each transect was divided into 0.5 m intervals and each interval received one randomly placed point for microhabitat measurement. At each point, I recorded average water velocity, water depth, substrate composition, distance from the nearest shore, and cover type. Water velocity was measured using a Swoffer 2100 current meter to the nearest 1 $cm \cdot s^{-1}$ with a top setting wading rod at 60% water depth, averaged over 15 s. Depth measurements (to the nearest 1 cm) were taken from the wading rod. Percentage substrate composition was visually classified within a 30-cm diameter circle laid on the stream bottom into fines (< 2 mm fines, detritus, clay/silt, and sand), and coarse, (> 64 mm) divisions. Cover types that provide velocity refuge, visual isolation or overhead cover (sensu Fausch 1993), were estimated as a percentage of transect length and included depth, turbulence (at the water surface so as to conceal fish presence), rock, undercut, aquatic and terrestrial vegetation.

Habitat use

Habitat use was determined using surface observations of YOY grayling on two occasions in each stream during the summer of 1999 (Table 5-2). Sampling individual grayling habitat use was difficult when fish were in close proximity to each other, particularly for the small-sized YOY. In such cases, the group of fish was sampled as

one observation. For small YOY, data were collected from the middle of the group, whereas for large grayling, data were collected from the leading fish. This difference in sampling protocol was meant to reflect the growing territorial behaviour of older and larger grayling. Fish were sampled in an upstream direction such that each grayling or group was minimally disturbed and only sampled once.

Once a fish or group was located, I recorded (as described above) average water velocity, total water depth, substrate composition, distance from the nearest shore, and cover type. In addition, for large grayling I measured the water velocity and depth at the fish's snout.

Differences in habitat characteristics associated with locations used by grayling versus those available were analyzed using Kruskal-Wallis one-way analysis of variance. I used nonparametric testing because habitat variables were generally not normally distributed and had unequal variances that could not be reconciled using transformations.

Model development

I developed resource selection functions (RSFs) for two sizes of YOY Arctic grayling in Polar-Vulture Creek, a natural Barrenland stream, to describe the relationship between microhabitat characteristics and the probability of habitat use. To develop the RSFs I used a combination of nonparametric generalized additive and parametric generalized linear models with binomial errors using S-plus software (Mathsoft 2002). As noted by Knapp and Preisler (1999), nonparametric models relax the assumptions of ordinary linear regression in two ways: (i) the distribution of the dependent variable need not be symmetric homoscedastic, and (ii) the relationship between the dependent and independent variables need not be linear. Relaxation of the linearity assumption between

the dependent and independent variables is accomplished using a spline smoothing function (e.g., cubic B-splines) to determine the model that best fits the independent variables. Although nonparametric logistic regression is useful describing the shape of response curves, parametric models are preferable in developing predictive models if they can provide an adequate fit to the data.

To develop the models I first examined correlations among independent variables and excluded highly correlated variables (i.e., $r > 0.7$; Hosmer and Lemeshow 2000). I then examined each remaining variable to assess which had additional nonlinear effects (Chi-squares; $P < 0.01$; MathSoft 2002) and plotted the response curves generated by the nonparametric regression for the significant independent variables. To develop a parametric model from the nonparametric model, I determined the appropriate generalized linear model (e.g., linear, polynomial) to approximate the nonparametric functions by examining the deviance explained (McCullagh and Nelder 1989). I based the final parametric model solely on the significant independent variables (ANOVA, $P < 0.05$) to ensure that only those independent variables with high explanatory power were included in the model. The relative importance of each variable was evaluated by calculating the Mallow's Cp statistic (MathSoft 2002). I calculated the cumulative coefficient of determination (R^2) by adding variables to the model in the order of their associated Cp value. I also calculated the percentage that each of the variables contributed to the total coefficient of determination.

Model validation

To evaluate the predictive success of the parametric models, I used a form of in-sample cross-validation for a withheld sample of habitat use data (Boyce et al. 2002). A model

with good prediction performance would be expected to correctly classify known habitat use locations in the natural stream (i.e., locations that should have a high probability of use). I used a training-to-testing ratio of 4:1, whereby model building was based on 80% of the habitat-use data, with the remaining 20% of the habitat-use data used for validation. Data for model building and validation were chosen randomly.

Assessment of habitat in the artificial stream

To evaluate habitat quality in the artificial stream I used the RSFs for small and large YOY grayling developed in the natural stream to predict probability of use for both known locations of habitat use and locations considered as available for use. For locations taken from habitat availability surveys, the model should predict a relatively large number of low probability of use scores and a small but unknown number of sites with a high probability of use (i.e., some availability locations should also be use locations). Thus, the availability data cannot, per se, be used to assess habitat quality, but can provide insight into the general quality of the habitat available. For known habitat-use locations, the RSFs should consistently predict high probability of use (similar to the cross-validation procedure) if habitat quality is good, but should produce an increasing proportion of low probability of use scores as habitat quality decreases in the artificial stream. For small YOY I used 341 random locations in the artificial stream to represent availability and 112 known use-locations. For the large YOY grayling, I used 351 availability-locations and 128 known use-locations.

Results

Habitat availability and use: Polar-Vulture stream

For most habitat variables, YOY grayling used a narrower range than what was available in Polar-Vulture. Available and used habitats differed for all variables for small grayling (Kruskal-Wallis, $P < 0.05$). Locations used by small YOY grayling were best described by shallow depths (14 cm ± 0.5 SE) and low velocities (2 $cm \cdot s^{-1}$ ± 0.2 SE) in association with larger amounts of detritus (90 % ± 2.3 SE), and small amounts of coarse substrates. Areas used by small YOY were inevitably close to the stream banks (0.4 m ± 0.02 SE).

In contrast to the smaller YOY, locations used by the larger YOY in Polar-Vulture did not generally differ from available locations except for water depth, detritus, fines, and undercut cover (Kruskal-Wallis, $P < 0.05$). Locations used by large YOY grayling were deeper (31 cm ± 1.0 SE) and contained smaller amounts of detritus (25% ± 4.1 SE) and fines (4% ± 1.2 SE) than available locations. Although not statistically significant, water velocities and aquatic vegetation were generally higher at sites used by large grayling than that available. These larger grayling also used locations farther out from stream banks (0.7 ± 0.03 m SE) than the smaller YOY.

Average snout depth of large YOY grayling in Polar-Vulture was only 11 cm ± 1.0 SE, or 35% of depth. As water depth increased beyond 40-50 cm grayling could be found higher off the streambed than 11 cm. The relationship between snout velocity, i.e., the water velocity at the fish snout, and average water velocity was considerably varied (range 0 - 1000 %, mode 100% of average velocity) when average velocities were low (0-10 $cm \cdot s^{-1}$): while at higher water velocities (11 – 20 $cm \cdot s^{-1}$) snout velocity was ca. 51% of average water velocity.

Resource selection: small young-of-the-year grayling

The nonparametric model for small grayling in Polar-Vulture indicated that water velocity, water depth, and detritus had significant nonlinear effects ($P < 0.01$). Based on the shapes of the response curves for these three variables, I used second-degree polynomials to approximate the nonparametric functional forms. In the final parametric model, four of the five habitat variables, water velocity, water depth, and amount of detritus and fines, had significant effects (ANOVA, $P < 0.05$; Table 5-3), in that order of importance. The four significant variables accounted for 55% the variance in habitat selection (Table 5-3). The parametric model for small YOY grayling is represented by the following equation:

$$\text{Logit line } \theta = 90.31(\text{velocity}) - 1374.77(\text{velocity})^2 - 68.20(\text{depth}) - 240.45(\text{depth})^2 + 7.89(\text{detritus}) - 4.41(\text{detritus})^2 - 7.82(\text{fine})$$

The response shapes for water depth and water velocity were highest at intermediate values, such that the probability of habitat for use was at a maximum at 13 cm and 2 $cm \cdot s^{-1}$, respectively (Fig. 5-2). The probability of use decreased with increasing amounts of fines, but increased with increasing detritus (Fig. 5-2).

Resource selection: large young-of-the-year grayling

The nonparametric model for large YOY in Polar-Vulture indicated that five of seven of the habitat variables had significant ($P < 0.01$) nonlinear effects, including water depth, the amount of detritus, and the cover variables water depth, aquatic vegetation, and rock. Based on the shapes of these response curves, I used second-degree polynomials to

approximate the nonparametric functional forms. In the final parametric model, eight of eleven habitat variables, the above five plus the amount of fines, terrestrial vegetation, and turbulence, had significant effects (ANOVA, $P < 0.05$; Table 5-4). Based on Mallow's Cp, the relative importance of the significant variables in explaining habitat use was water depth > detritus > depth as cover > terrestrial vegetation > rock > turbulence > fine > aquatic vegetation. The eight variables accounted for 36% the variance in habitat selection (Table 5-4). The parametric model for large YOY grayling is represented by the following equation:

$$\text{Logit line } \theta = 25.10(\text{water depth}) - 20.94(\text{water depth})^2 - 3.26(\text{detritus}) + 1.31(\text{detritus})^2 - 15.14(\text{depth}) + 9.62(\text{depth})^2 + 9.37(\text{terrestrial vegetation}) - 33.65(\text{terrestrial vegetation})^2 + 1.51(\text{rock}) - 13.22(\text{rock})^2 - 8.12(\text{turbulence}) + 2.64(\text{fine}) - 1.04(\text{aquatic vegetation}) - 6.66(\text{aquatic vegetation})^2$$

The response shape for water depth and water velocity (although the latter was not significant in the model) indicated that the probability of habitat use is at a maximum at intermediate values of 58 cm and 10 $cm \cdot s^{-1}$, respectively (Fig. 5-2). Similarly the probability of habitat use for the variables detritus, and rock and aquatic vegetation cover is optimal at intermediate values, 30%, 19%, and 24%, respectively. The probability of use for fines and coarse substrates, and cover variables depth, turbulence, and terrestrial vegetation all increased with increasing values (Fig. 5-2).

Model validation

The in-sample cross-validation procedure for the withheld sample of data indicated that the parametric model generally performed well, correctly classifying 75% and 71% of known use locations for small and large YOY, respectively. Because the model predictions indicated that probabilities of use were either very high (e.g., 0.98) or very low (e.g., 0.0001) I did not area-adjust the frequencies for habitat availability (Boyce et al. 2002).

Assessment of habitat in the artificial stream

The resource selection function developed for small YOY from the natural stream indicated that the habitat quality in the artificial stream was generally good, in that a large proportion (71%) of sites used by small grayling were predicted with high probability (> 0.9) to be used (Fig. 5-3). In contrast, only a small proportion (14%) of locations used by large YOY received high probability of use values; indeed, many locations (43%) used by large YOY in the artificial stream generated low probability of use values (< 0.1) from the RSF (Fig. 5-3), suggesting that habitat quality in the artificial stream was poor.

Discussion

Habitat use typically involves a small subset of available habitat. Organisms select habitats that provide the greatest gains, in terms of survival and reproduction, thus, habitat choice has or is an evolutionary consequence (Boyce and McDonald 1999). For stream-dwelling fish, some locations are energetically more profitable than others (Fausch 1984; Hughes and Dill 1990) and it is generally believed that these locations have a higher probability of being used.

Profitability of a given habitat, however, is frequently size dependent among stream-dwelling salmonids (Sempeski and Gaudin 1995, Huusko 2003). As was evident from the resource selection functions, I also found that small and large YOY grayling respond differently to available habitat. Small YOY grayling selected locations with shallow depths, e.g., near-bank and pocket-water habitats in riffles common in natural Barrenland streams. These locations were also typically in association with low water velocities, related to the limited swimming ability of these small fish (Scott 1985). As YOY grayling grow (> 25 mm) and become better swimmers and increasingly territorial (Kratt and Smith 1979), they shift to the main channel where greater depths and higher mean water velocities are available. At this stage, grayling use velocity refugia associated with deep pools and created by large boulders along the thalweg, from which they can feed opportunistically on drifting organisms (Fausch 1984; Hughes and Dill 1990). Habitat selection by small YOY, therefore, highlights the importance of slow moving shallow water, often unfortunately called "dead-zones" (Gaudin and Sempeski 2001), the absence of which could lead to high mortality during flooding (Armstrong 1986). Habitat selection by the larger YOY, in contrast, highlights the importance of midstream cover, e.g., rocks and aquatic vegetation that provide velocity refuge, visual isolation, and overhead cover.

Water velocity, although frequently found to be an important determinant in habitat choice by stream fishes and important for small YOY in this study, was not a significant variable in the large young-of-the-year RSF. One possible reason for this lack of statistical significance is a lack of difference between availability and use, i.e., habitat use was proportional to habitat availability. This seems unlikely given the work of Fausch

(1984) and others, so it is also possible that velocity refugia created by boulders, common in Barrenland streams, bias the measurement of average water velocity at 60% depth. In other studies, average water column velocity may be of predictive value because it is highly correlated with snout velocity. In this study, snout velocity was generally some fraction of average water velocity at locations used by large YOY grayling, particularly at higher water velocities, suggesting the importance of velocity refugia to habitat selection. As such, average (i.e., depth-averaged) water velocity may be a poor measure of actual habitat availability and use.

Similar to snout velocity, snout depth was typically a small fraction of total water depth. The relationship between snout and water depth increased proportionately until a water depth of 0.4-0.5 m was reached. At that point, grayling could be found relatively higher off the stream bed, possibly because some threshold of predator avoidance is reached, after which grayling can move off the bottom with little increased risk of predation from, e.g., birds, or perhaps related to optimal foraging.

The relative unimportance of substrate characteristics, which are often important in other studies (e.g. Knapp and Preisler 1999), was surprising. However, Barrenland streams are generally stable, permafrost-bound, and boulder-dominated colluvial systems, i.e., fluvial process are relatively ineffective at removing material deposited on the valley floor. As a consequence, substrates in Barrenland streams are poorly sorted in comparison to alluvial streams, where water velocities sort substrate material based on particle size, producing a correlation between velocity and substrate (Morisawa 1968). In contrast, I found little correlation between substrate and average water velocity in Polar-Vulture. Another reason for the limited importance of substrate in the RSFs is that

selection of a location does not likely reflect the substrate composition at that location, per se, but the substrate of an area upstream that supplies drifting macroinvertebrates upon which grayling feed (Chapter III). This differs from habitat selection by spawning stream fishes, where the characteristics of substrate at a site are critical to the development and survival of eggs (Chapman 1988; Knapp and Preisler 1999).

Cover-related habitat variables, including water depth, aquatic and terrestrial vegetation, rock, and water turbulence, were important determinants of probability of use by larger YOY grayling in Polar-Vulture. As expected, the probability of habitat use typically increased with increasing cover. Unexpected was the hump-shaped form of selection for rock and aquatic vegetation. Grayling often selected a combination of cover types, with no one type being dominant. However, some cover types likely serve more than one function. For example, aquatic vegetation type can likely provide overhead cover, visual isolation, and velocity refugia. Structures that provide velocity refuge allow fish to hold low velocity positions adjacent to faster water currents and thus maximize their energy intake from drifting food items while minimizing the cost of swimming to maintain position (Fausch and White 1981; Fausch 1984). Structure may also provide visual isolation, decreasing energetically costly agonistic behaviour and allowing for higher fish densities, consistent with what I observed in Polar-Vulture (Chapter IV). Overhead cover can decrease the amount of energy invested in vigilance against predators.

Model validation

Ideal models for habitat selection would incorporate all the important characteristics of fish habitat use (realism), account for a large percentage of variation in habitat use (precision), and be based on years of data from a broad geographic range to incorporate

environmental variation (generality). Simultaneously maximizing all three of these characteristics in biological models is difficult (Levins 1966). Nevertheless, resource managers are charged with the task of evaluating changes to a variety of stream habitat in a timely manner, often in the absence of site-specific data. It is generally not logistically and economically possible, however, to develop resource selection functions, case by case, for all environmental conditions that may influence fish habitat use (Mäki-Petäys et al. 2002). As result, models must be used to predict the effects of modification in systems other than those for which they were developed. The predictive power usually decreases when models are tested in novel environments. Differences habitat availability alone may affect habitat selection, particularly if the spectrum of habitat types examined is limited. A habitat may become used more as it becomes more available, similar to a functional response (Boyce et al. 2002). To further complicate prediction, habitat use may be affected by other factors, such as food availability, competition, predation (e.g., Fausch 1984; Orth 1987; Biro et al. 2003), water temperature and season (Mäki-Petäys et al. 1997), time of day (Johnson and Covich 2000), and discharge (Holm et al. 2001). Despite these difficulties, the transferability of habitat criteria for Atlantic salmon (Salmo salar) was conceivable on regional and possibly "universal" scales (Mäki-Petäys et al. 2002). Although I did not examine transferability at either of these scales, it was encouraging to note that both RSF models were good predictors of habitat use as demonstrated by the cross-validation results in Polar-Vulture. This is particularly true considering that, as with any RSF using habitat availability and use data, group membership is uncertain, i.e., use is a subset of availability and thus not unique, unlike

the used-vs.-unused designs (Manly et al. 1993; Boyce et al. 2002). As result, the strength of relationships in this study could actually be muted.

Assessment of habitat in the artificial stream

As part of a larger objective to evaluate the effectiveness of the artificial stream as habitat compensation, I used the RSFs for small and large YOY grayling from Polar-Vulture, the natural stream, to assess the quality of nursery habitat for YOY grayling in the nearby artificial stream. Results of my assessment differed depending on the size-class of grayling examined. Many locations in the artificial stream where I observed small YOY grayling were, in fact, predicted by my RSFs to have a high probability of being used. In contrast, many locations where I observed large YOY were predicted to have low probability of use. Although these results can be partly explained within the context of an ontogenic shift in habitat requirements of YOY grayling, I suggest that they also reflect the poor productive capacity of the artificial stream.

My RSFs suggest that the habitat requirements of small YOY are relatively simple and thus more easily met than those of the larger YOY, which could account for the differences in predicted habitat quality. As indicated by their RSF model, small YOY select shallow, slow moving water with high amounts of detritus. They did not appear to use any cover; instead, they distributed themselves into small schools as a basic anti-predation tactic. The lower proportion of the variance in habitat use explained by the RSF for larger YOY, despite more variables being included into the model, suggests that their habitat requirements are more complex. For example, territoriality and the use of various forms of cover were evident in habitat selection by larger grayling (Kratt and Smith 1979; N. Jones, pers. obs).

The effects of poor habitat available for large YOY can be seen in the limited ability of the artificial stream to produce grayling biomass in comparison to natural streams e.g., Polar-Vulture (Chapter IV). The average mass of young-of-the-year grayling at the end of summer (1998-2001) was significantly lower in the artificial stream than in natural streams (Chapter IV). This large difference in growth, in concert with differences in YOY grayling density, meant that end-of-season standing crop in the artificial stream was only 40% of that found in Polar-Vulture (Chapter IV). Although I previously emphasized the low amounts allochthonous organic matter in the artificial stream in limiting the productivity of benthic invertebrates, and in turn, YOY grayling (Chapter IV), I also had suggested that the limited quantity and quality of physical habitat likely contributed to the poor growth of YOY in the artificial stream. My results here strongly support that suggestion, and point to a failure of the artificial stream to provide habitat for larger YOY grayling, including velocity refugia, visual isolation, and overhead cover (Fausch 1993). Nevertheless, there remains the possibility that the model developed for large YOY grayling in Polar-Vulture simply does not transfer to other streams, including (or especially) the artificial stream where aquatic and terrestrial vegetation, common and important elements in the natural stream, were extremely rare.

This study is the first to quantitatively measure and model habitat use and selection by YOY Arctic grayling and, given their importance in Barrenland streams (Chapter II), represents a start in understanding fish-habitat relations in the Arctic. The resource selection functions also prove valuable as a habitat assessment technique. Larger YOY were forced to use habitat that would not normally be used in the natural streams. This is consistent with the poor growth, density, and biomass of YOY observed in the artificial

stream in comparison to that observed in natural streams. Although the artificial stream has restored watershed connectivity for fish migration and provided suitable spawning areas (Chapter IV), nursery habitats are poor, particularly with regards to larger YOY grayling.

The application of these models in the context of habitat management remains challenging, particularly in the dynamic environments of lotic habitats, and supports application of the precautionary principle. The use of GIS and river flow models, such as physical habitat simulation (PHABSIM; Bovee 1986) and 2-dimensional flow models (Ghanem et al. 1996), not only represents interesting ecohydraulic links, but offer much opportunity for developing defensible methods for fish habitat assessment in rivers (e.g., Minns et al. 1995).

Literature Cited

Armstrong, R.H. 1986. A review of Arctic grayling studies in Alaska, 1952 – 1982. Biological Papers of University of Alaska. Number 23.

Benaka, L., editor. 1999. Fish habitat: essential fish habitat and rehabilitation. American Fisheries Society, Symposium 22, Bethesda, Maryland.

Biro, P.A., Post, J.R., and Parkinson, E.A. 2003. Population consequences of a predator-induced habitat shift by trout in whole-lake experiments. Ecology 84: 691-700.

Boyce, M.S., and McDonald, L.L. 1999. Relating populations to habitats using resource selection functions. Trends in Ecology and Evolution 14: 268-272.

Boyce, M.S., Vernier, P.R., Nielsen, S.E., and Schmiegelow, F.K.A. 2002. Evaluating resource selection functions. Ecological Modelling 157: 281-300.

Bovee, K.D., 1986. Development and evaluation of habitat suitability criteria for use in the instream flow incremental methodology. U.S. Fish and Wildlife Service Biological Report 86. 235 pp.

Chapman, D.W. 1988. Critical review of variables used to define effects of fines in redds of large salmonids. Trans. Amer. Fish. Soc. 117: 1-21.

Department of Fisheries and Oceans (DFO). 1986. The Department of Fisheries and Oceans policy for the management of fish habitat. Communications Directorate, Fisheries and Oceans, Ottawa, Ontario, Canada.

Fausch, K.D. 1984. Profitable stream positions for salmonids: relating specific growth rate to net energy gain. Can. J. Fish. Aquat. Sci. 62: 441-451.

Fausch, K.D. 1993. Experimental analysis of microhabitat selection by juvenile steelhead (*Oncorhynchus mykiss*) and coho salmon (*O. kisutch*) in a British Columbia stream. Can. J. Fish. Aquat. Sci. 50: 1198-1207.

Fausch, K.D., and White, R.J. 1981. Competition between brook trout (*Salvelinus fontinalis*) and brown trout (*Salmo trutta*) for positions in a Michigan stream. Can. J. Fish. Aquat. Sci. 38: 1220-1227.

Gaudin, P., and Sempeski, P. 2001. The role of river bank habitat in the early life of fish: The example of grayling, *Thymallus thymallus*. Ecohydro. Hydrobio. 1: 203-208.

Ghanem, A.H., Steffler, P.M., Hicks F.E., and Katopodis, C. 1996.Two dimensional finite element flow modeling of physical fish habitat. Regulated Rivers: Research and Management, 12: 185-200.

Holm, D.J., Armstrong, J., and Gilvear, D.J. 2001. Investigating a major assumption of predictive in-stream habitats models: is water velocity preference of juvenile Atlantic salmon independent of stream discharge. J. Fish Bio. 59: 1653-1666

Hosmer, D.W., Jr., and Lemeshow, S. 1989. Applied logistic regression. John Wiley & Sons, New York, USA

Hughes, N.F., and Dill, L.M. 1990. Position choice by drift-feeding salmonids: a model and test for Arctic grayling (*Thymallus arcticus*) in subarctic mountain stream, interior Alaska. Can. J. Fish. Aquat. Sci. 47: 2039-2048.

Hubert, W.A., R.S. Helzner, L.A. Lee, and P.C. Nelson. 1985. Habitat suitability index models and instream flow suitability curve: Arctic grayling riverine populations. U.S. Fish and Wildlife Service. FWS/OBS-82/10.110

Huusko, N.M. 2003. Size-related changes in habitat selection by larval grayling (*Thymallus thymallus* L.). Eco. Freshwater Fish 12: 127-133.

Johnson, S.H., and Covich, A.P. 2000. The importance of night-time observations for determining habitat references of stream biota. Reg. Rivers: Res. Manage. 16: 91-99.

Knapp, R.A., and Preisler, H.K. 1999. Is it possible to predict habitat use by spawning salmonids? A test using California golden trout (*Oncorhynchus mykiss aguabonita*). Can. J. Fish. Aquat. Sci. 56: 1576-1584

Kratt, L.F., and Smith, R.J.F. 1979. Agonistic behaviour of age 0, and age 1 and non-breeding adult Arctic grayling Thymallus arcticus (Pallas). J. Fish Bio. 15: 389-404.

Levins, R. 1966. The strategy of model building in population biology. Am. Sci. 54: 421-431.

Mäki-Petäys, A., Huusko, A., Erkinaro, J., and Muotka, T. 2002. Transferability of habitat suitability criteria of juvenile Atlantic salmon (*Salmo salar*). Can. J. Fish. Aquat. Sci. 59: 218-228.

Maki-Petäys, A., Muotka, T., Huusko, A., Tikkanen, P., and Kreivi P. 1997. Seasonal changes in habitat use and preference by juvenile brown trout Salmo trutta in a northern boreal river. Can. J. Fish. Aquat. Sci. 54: 520-530.

Manly, B.F.J., McDonald, L.L., and Thomas, D.L. 1993. Resource selection by animals: statistical design and analysis for field studies. Chapman and Hall, London, UK.

MathSoft. 2002. S-PLUS 6 for windows user's guide, Insightful Corporation, Seattle, USA.

McCullagh, P., and Nelder, J.A. 1989. Generalized linear models. Second edition Monographs on Statistics and Applied Probability 37. Chapman and Hall, London, UK.

Minns, C.K., Meisner, J.D., Moore, J.E., Greig, L.A., and Randall, R.G. 1995. Defensible methods for pre- and post-development assessment of fish habitat in the Great Lakes. A prototype methodology for headlands and offshore structures. Can. MS Rep. Fish. Aquat. Sci. 2328.

Minns, C.K., Kelso, J.R.M., and Randall, R.G. 1996. Detecting the response of fish to habitat alterations in freshwater systems. Can. J. Fish. Aquat. Sci. 53(Suppl. 1): 403-414.

Morisawa, M. 1968. Streams: their dynamics and morphology. McGraw-Hill. NY, USA.

Orth, D.J. 1987. Ecological consideration in the development and application of instream flow-habitat models. Reg. Rivers Res. Manage. 1: 171-181

Schindler, D. W. 2001. The cumulative effects of climate warming and other human stresses on Canadian freshwaters in the new millennium. Can. J. Fish. Aquat. Sci. 58: 18-29.

Sempeski, P., and Gaudin, P. 1995. Size-related changes in diel distribution of young grayling (*Thymallus thymallus*). Can. J. Fish. Aquat. Sci. 52: 1842-1848.

U.S. Fish and Wildlife Service. 1981. Standards for the development of habitat suitability index models United States Fish and Wildlife Service, Release No. 1-81, 103 ESM

Table 5-1. Physical characteristics of Polar-Vulture and the artificial stream, Northwest Territories, Canada.

Stream	Length (m)	Slope %	Sinuosity	Bankfull width (m)	Bankfull depth (cm)	Mean velocity ($cm \cdot s^{-1}$)	% fines[a]	% coarse[b]
Polar-Vulture	700	1.4	1.23	2.7	44	13	20	55
Artificial	700	0.9	1.02	6.6	44	21	40	32

[a] includes clay, silt, and sand (< 2 mm) [b] includes cobble and boulder (64 – 256 mm >).

Table 5-2. Dates and sizes of young-of-the-year (YOY) Arctic grayling when habitat use and availability observations were made in the Polar-Vulture (PV) and the artificial stream (ART) in 1999.

	Small YOY		Large YOY	
Observation dates	10-15 July		13-19 August	
Stream	PV	ART	PV	ART
Number of individual fish	474	1503	172	310
Number of groups of fish	102	140	89	160
YOY fork length (mm)				
Mean ± standard error	18 (0.2)	15 (0.1)	46 (0.4)	42 (0.4)
Range	15-21	13-18	38-57	32-52
YOY mass (g)				
Mean ± standard error	0.04 (0.001)	0.01 (0.001)	0.89 (0.03)	0.64 (0.02)
Range	0.02-0.09	0.01-0.03	0.37-1.78	0.24-0.99

Table 5-3. Analysis of deviance table showing the statistical significance (P value) and R^2 values of the independent variables in the parametric logistic regression model for small young-of-the-year Arctic grayling in Polar-Vulture, a natural Barrenland stream. % of R^2 is the percentage that each variable contributed to the total coefficient of determination. Italics indicate variables that had significant nonlinear effects. Null model residual deviance was 512 with 727 degrees freedom.

Habitat variable	Deviance explained	df	P	Cumulative R^2	% of R^2
Water velocity	126.8	725	< 0.0001	25	45
Water depth	91.1	723	< 0.0001	43	32
Detritus	58.0	721	< 0.0001	54	21
Fine	5.5	720	0.0187	55	2
Coarse	0.1	719	0.7915	55	0

Table 5-4. Analysis of deviance table showing the statistical significance (P value) and R^2 values of the independent variables in the parametric logistic regression model for large young-of-the-year Arctic grayling in Polar-Vulture, a natural Barrenland stream. % of R^2 is the percentage that each of the variable contributed to the total coefficient of determination. Italics indicate variables that had significant nonlinear effects. Null model residual deviance was 426 with 547 degrees freedom.

Habitat variable	Deviance explained	df	P	Cumulative R^2	% of R^2
Water depth	55.9	545	< 0.0001	13	35
Detritus	26.0	543	< 0.0001	19	16
Depth	15.3	541	0.0005	23	10
Turbulence	18.8	535	0.0001	32	12
Aquatic vegetation	13.2	531	0.0014	37	8
Terrestrial vegetation	12.3	539	0.0021	26	8
Rock	7.2	537	0.0276	27	4
Fine	4.3	534	0.0382	33	3
Coarse	3.4	533	0.0636	34	2
Undercut	3.3	529	0.1895	37	2
Water velocity	0.4	528	0.5459	38	0

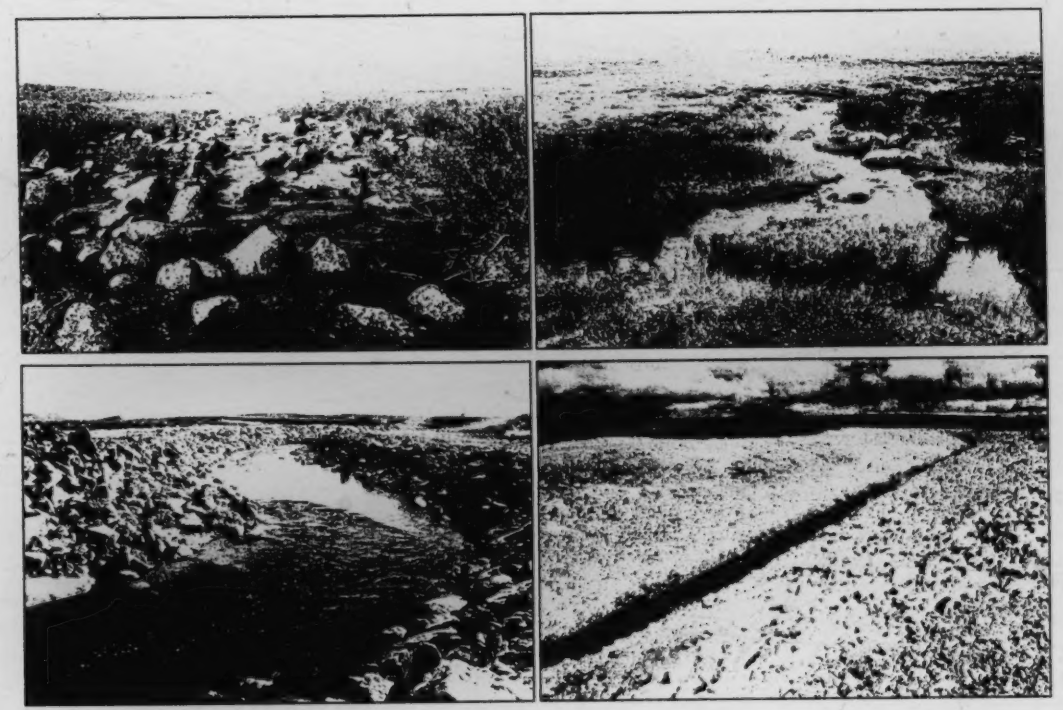

Figure 5-1. Two views of Polar-Vulture, the natural stream (top), and of the artificial stream (bottom).

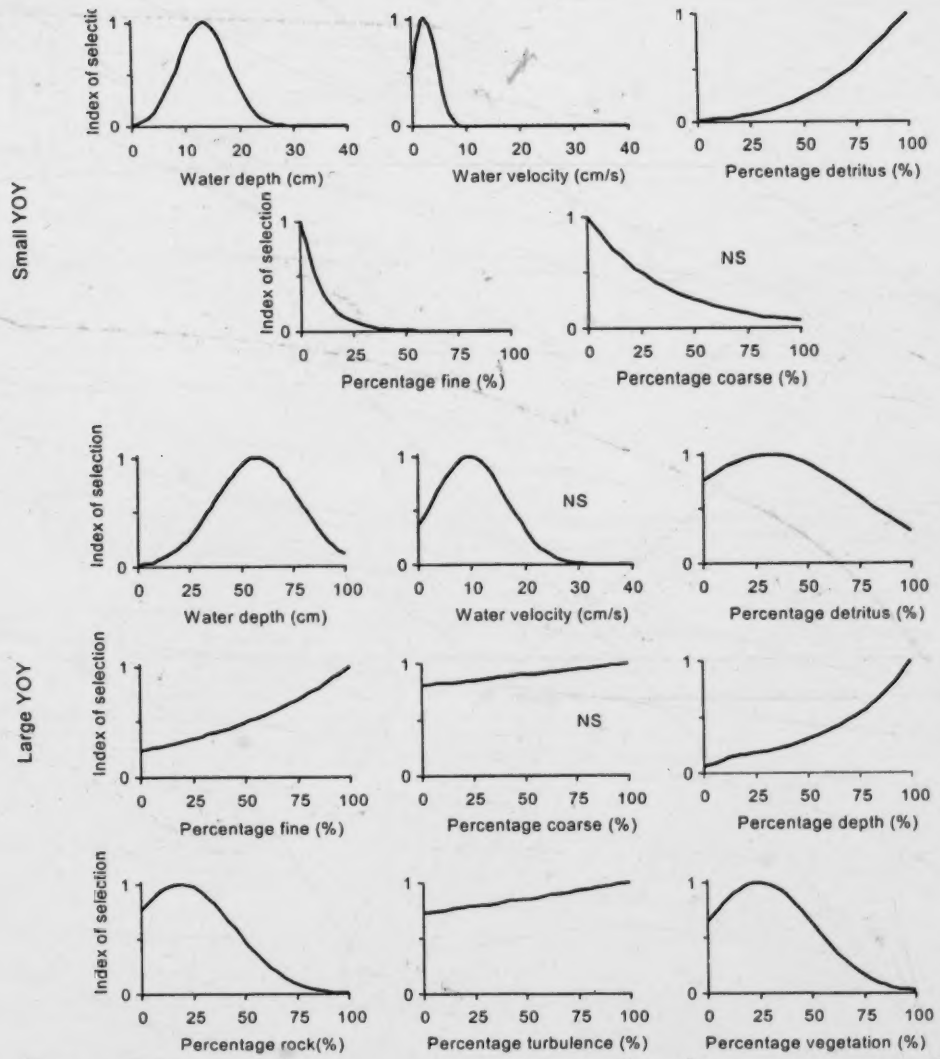

Figure 5-2. Resource selection curves for small and large young-of-the-year Arctic grayling in a natural Barrenlands stream (Polar-Vulture). Some variables did not significantly (NS) contribute to the models but were still of general interest. Vegetation plot (bottom right-hand corner) represents aquatic (solid black lines) and terrestrial vegetation (solid grey lines). Index of selection is standardized to range from high (1) to low (0) probability of use.

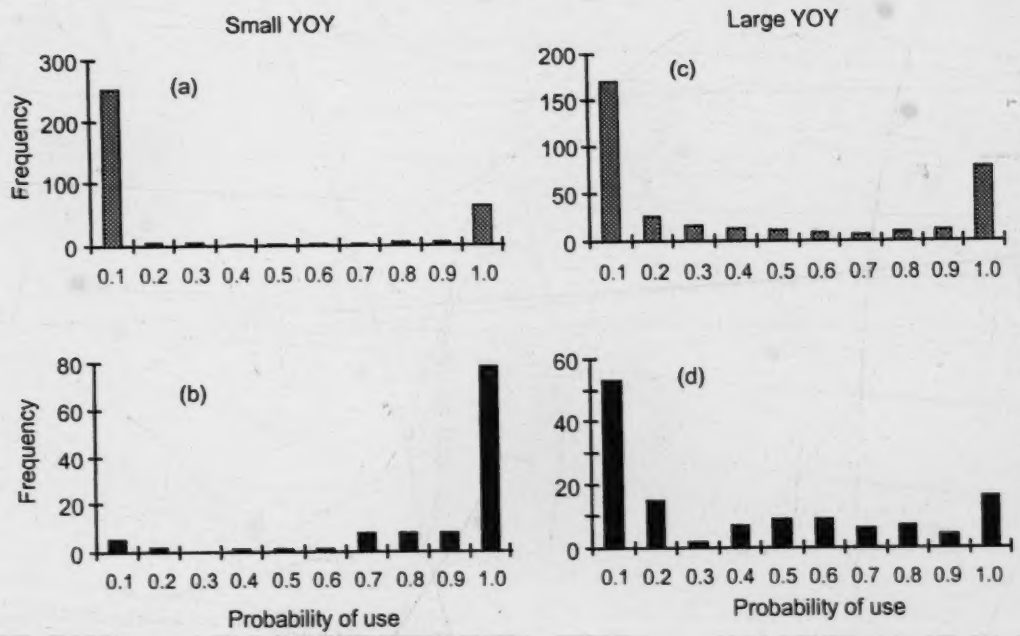

Figure 5-3. Predicted probability of use for habitat that was available to (a,c) and used by (b,d) small (a,b) and large (c,d) young-of-the-year Arctic grayling in the artificial stream, based on resource selection functions from the natural Barrenland stream (Polar-Vulture).

Chapter VI: Enhancing Productive Capacity in the Canadian Arctic: Assessing the Effectiveness of Instream Habitat Structures in Habitat Compensation

Introduction

Traditional approaches to stream restoration focus on relatively short-lived (ca. 5 year), small-scale physical prescriptions, including the development of instream structures to enhance habitat quality and quantity. Many of these instream habitat structures, however, do not address fundamental problems within the catchment (e.g., lack of riparian vegetation) and consequently, such approaches typically fail in the long run (Beechie and Bolton 1999). Such actions can nevertheless be beneficial while natural habitat-forming processes rebuild fish habitat (Roni et al. 2002). Habitat structures are typically designed to enhance fish production by providing a suitable combination of physical conditions. More specifically, successful habitat structures likely provide important features associated with trade-offs between foraging and predation risk: (i) velocity refuge, (ii) visual isolation, and (iii) overhead cover (Fausch 1993). Frequently, habitat enhancement structures are designed for a particular life history stage that appears to be limited (e.g., spawning or juvenile habitat). Less frequent are instream structures that focus on non-fish components, such as the production of invertebrates for fish consumption. For whatever their use, scientific evaluations of restoration efforts are needed, for only then we can begin to learn from our collective experiences (Bradshaw 1996; Minns et al. 1996).

The focus on instream habitat structures is based on the notion that the supply and suitability of habitat ultimately limit fish populations (Minns 1997). However, relationships between physical characteristics of streams, habitat productivity, and fish production are often poorly understood. This poor understanding between habitat and fish production is particularly true in the Arctic. Unlike temperate regions (see White 1996), few attempts at stream restoration or enhancement have been made in the north. However, the need for proven techniques and a better understanding of high latitude stream ecology has never been more pressing. In the last 50 years, arctic regions have experienced a steady expansion in both the development of their natural resources and in environmental impacts (Schindler 2001). However, increasing pressures have not been matched by increases in research directed toward mitigating ecosystem impacts.

In the present study, I examined the effectiveness of four types of habitat structures (ramps, v-weirs, vanes, and groins) at increasing the productive capacity for Arctic grayling (*Thymallus arcticus* Pallas) and other fish in a 3.4-km artificial stream created as part of a regulatory program to compensate for fish habitat lost in development (DFO 1986). To date, there have been few serious attempts to restore or enhance fish habitat specifically for grayling (Stirling 1979; Hunter and Fernet 1990) or in high latitude streams (Armstrong 1986; Northcote 1995). More generally, because the "as built" artificial stream largely lacked typical habitat features produced by natural stream processes, the addition of physical habitat provides an excellent opportunity to examine the contributions that instream structures can make to stream productive capacity. Employing a modified before-after-control-impact (BACI) design (Stewart-Oaten et al.

1986), I quantified changes in fish density, biomass, and growth at two spatial scales, in the immediate area of the structures and for the artificial stream as a whole.

Study System

The Artificial stream

In 1991, diamonds were discovered in the remote region of the Northwest Territories of Canada known as the Barrenlands. In preparation for mineral extraction at the first of several mines scheduled for development, two lakes and their tributary streams, set within a larger chain of lakes, were drained. A habitat compensation agreement with the Department of Fisheries and Oceans required the mine to construct a artificial stream to restore watershed connectivity for fish migration and to provide spawning and nursery habitats to offset the losses in stream habitat. Since 1997, water has been diverted around the two lakes, now open-pit mines, through the artificial stream (Fig. 6-1). Starting at the end of the artificial stream's first full year in operation (1998), habitat structures were also added to enhance fish production. Habitat was built with particular focus on Arctic grayling (*Thymallus arcticus* Pallas), as they dominate fish communities in the Barrenlands (Chapter II).

Despite its 3.4-km length (versus a median of 380 m for 20 natural Barrenland streams; Chapter II), the artificial stream originally had a limited number of habitat types. The artificial stream is often constrained by steep (10-90°) and high (2-10 m) banks, with a single channel throughout its entire length (Fig. 6-2). Naturally occurring wetlands and boulder gardens are absent while riffles and pools are few; about half the artificial stream length consisted of featureless sandy flats. Fine sediment, i.e., silt, clay, and sand, dominate 44% of the substrate composition in the artificial stream, versus only 14% in

natural streams (Chapter IV). Rock lines a largely unvegetated riparian zone, whereas natural streams have riparian zones dominated by dwarf birch (*Betula glandulosa* Michaux), willow (*Salix spp.),* and sedge (*Carex spp.*). Aquatic vegetation common in natural streams (e.g., bur-reed, *Sparganium hyperboreum* and mare's-tail, *Hippuris vulgaris*) is also very rare in the artificial stream (Fig. 6-2).

Habitat Structures

Because the diversity of habitat for YOY Arctic grayling was low in the artificial stream, managers believed that the addition of habitat structures would enhance the artificial stream's productive capacity. At the upstream end of the artificial stream, five groins and two ramps were added, while six V-weirs and two vanes were added to the downstream end of the artificial stream (see Fig. 6-3). Each structure was built with aggregate removed from eskers in the region. Because large woody debris is not naturally found in tundra regions, no wood was used in structure construction. Descriptions of each structure type, the types of habitat it provides, the function of those habitats with respect to the needs of adult and YOY Arctic grayling, and the general influence of each structure on water velocities and depths are summarized in Table 6-1.

Methods

My assessment of structure effectiveness included examinations at two spatial scales: in the immediate area of each structure (mesohabitat) and the artificial stream as a whole (macrohabitat). For structure-scale assessments, I quantified effects of structures on grayling density, biomass, and growth rate using adjacent unmodified sections of artificial stream as controls (*sensu* Chapman 1999). At the scale of the whole stream, the first summer (1998) represented the "before" or pre-manipulation period and the

following three summers (1999-2001) post-manipulation. Three nearby natural streams, Polar-Vulture (PV), Pigeon (PG), and Polar-Panda (PP), were used as references during all or part of the study period.

Structure-Scale Assessment

Fish density and biomass

I estimated total fish density (fish·m^{-3}) and biomass (g·m^{-3}) using the three-pass removal method (Zippin 1958) twice at each structure, on 20 July and 20 August 2000, to incorporate changes in habitat use with increasing YOY grayling size. Larval grayling were found swimming freely on 1 July 1999, with yolk sacs still visible. Later that summer, the majority out-migrated to overwinter in nearby lakes by late August 2000. During electrofishing, block nets (5 mm mesh) were used to prevent immigration and emigration and care was taken during net placement not to displace fish. Control sections were located upstream and or downstream (~10 m) of sections with structures; some control sections were shared among several structures that were in close proximity to each other. There were three control sections of stream for each structure type studied. In August 2000, the five groin structures were electrofished as a unit because fish densities were likely too low for proper estimation. Captured fish were identified, enumerated, weighed (± 0.01 g), measured (fork length ± 1 mm), and released. Section volume, i.e., mean depth from 5-10 transects perpendicular to flow multiplied by mean width and section length, was determined for each section shortly after being fished (Table 6-2). Computations for population estimates were made separately for Arctic grayling, slimy sculpin (*Cottus cognatus* Richardson), and burbot (*Lota lota* L.) using the program CAPTURE V.1 (White et al. 1982). For each species in each section, I

estimated total fish biomass by multiplying the mean individual mass for a species by the number of fish estimated for that section of stream. Upwards of 90% of the estimated numbers of fish were typically captured in each fished section of stream. For each structure type, I used a combination of t-tests (vanes, v-weirs, and groins) and one-sample hypothesis testing (ramps) with Bonferroni adjustment to determine if fish densities and biomass differed between manipulated and non-control sections of stream. Because qualitative observations during sampling indicated large differences in fish density between the two ramps, they were analyzed separately.

YOY grayling growth

I used mass and length data from the previously described sampling at structures and control sections of stream to determine if structures affected the growth of YOY grayling. This comparison was conducted only for the 20 July sample date, three weeks after swim-up, because grayling movements become too extensive later in the summer, which would prevent accurate assessment of the effects of the structures. I used a combination of t-tests (vanes, v-weirs, and groins) and one-sample hypothesis testing (ramps) to determine if the mean mass of YOY grayling differed between sections of stream with and without structures. As above, there were three control sections of stream for each structure type examined.

Artificial stream-Scale Assessment

Between 1998 and 2001, I conducted analogous assessments of fish density and biomass, and of YOY grayling growth, at the whole-stream scale to determine if the addition of habitat structures in the artificial stream had any effects at this larger scale. Both spatial (artificial stream vs. natural streams) and temporal (before vs. after structure addition)

comparisons were used in the assessments. Additional natural streams (Pigeon and Polar-Panda) were sampled in 1999, 2000, and 2001.

Fish density and biomass

I estimated total fish density (fish·m^{-3}) and biomass (g·m^{-3}) in the artificial stream and nearby Polar-Vulture stream in late-July 1998-2000, using previously described methods. In the artificial stream, fourteen sample sections of stream, ranging 60-100 m in length and typically incorporating several habitat structures, were electrofished per year. In the shorter, 700-m long Polar-Vulture, ten sample sections of stream, ranging 30-75 m in length, were electrofished per year. In both streams, roughly the same sections were sampled in each year. Upwards of 75% of the estimated numbers of fish were typically captured in each fished section. I used general linear modeling (GLM) to compare fish densities and biomass between the artificial stream and Polar-Vulture stream. Main effects included stream (natural vs. artificial stream), year (1998-2000), and habitat type (pool and riffle). A significant interaction term (year-by-stream) in the BACI model suggests an effect of structures (Stewart-Oaten et al. 1986). To determine where, if any, interactions were occurring I used GLM to compare each pair of years per model i.e., 1998 vs. 1999, and 1998 vs. 2000. For comparative purposes, I also calculated the percentage difference in density and biomass between the artificial stream and Polar-Vulture for each year and compared values among years.

YOY grayling growth

The specific growth rate (SGR) of YOY grayling was estimated for the artificial stream, Polar-Vulture, Pigeon, and Polar-Panda streams by the equation:

$$SGR = \frac{\ln M_2 - \ln M_1}{t_2 - t_1} \text{ x } 100\%$$

where M_1 and M_2 are the mean mass of grayling shortly after swim-up (14 mm total length) in early July and shortly before out-migration in late August, respectively, and t_1 and t_2 are Julian dates for those two samplings. I used GLM to determine if growth rates differed between the artificial stream and Polar-Vulture stream, since it was the only natural stream sampled prior to construction of structures in the artificial stream. Main effects included stream and year. A significant year-by-stream interaction term, suggesting an effect of the structures, was followed by GLM comparing each pair of years per model to determine where interaction effects were occurring. Where I did not have a complete four-year data set (Pigeon and Polar-Panda streams), I used ANOVA to determine if growth rates differed between the artificial stream and natural streams within each year. I also calculated the percentage difference in SGR between the artificial stream and the mean SGR from the natural streams.

For all statistical testing I used the Kolmogorov-Smirnov test to examine data for normality and Levene's median test for homogeneity of variances. Where needed, I log-transformed data. For all statistical tests I used 0.05 as a critical level of significance following Bonferroni adjustment when required to reduce experimentwise error rate.

Results

Upwards of 80% and 52% of fish in the artificial stream were YOY grayling in July and August, respectively; the remainder consisted of slimy sculpin and burbot. Compositions in the reference streams were similar (Chapter IV). There was a positive relationship

between YOY grayling density and distance downstream (Fig. 6-4a). In contrast, there was a strong negative relationship between the size of YOY grayling and their distance downstream in the artificial stream (Fig. 6-4b), that is, fish closer to the upstream lake outlet were larger. Highest grayling densities occurred in the last 700 m of stream, where the majority of grayling spawning took place.

Structure-Scale Assessment

Habitat structures maintained their form during the study, even after an estimated 1:100 year flood in the spring of 1999. This large flood was the first to scour substrata sufficiently to redistribute sediment throughout the artificial stream and amongst the structures.

Fish density and biomass

Fish density in late July was higher at all structure types, especially ramp1, than at control sites (Fig. 6-5a). With the exception of groins, fish biomass was also higher at all structures. By late August, however, densities and biomasses were reduced at both control and structure sites. Only at ramp1 were fish densities and biomasses greater than at control sites (Fig. 6-5b).

YOY grayling growth

Despite higher densities and total fish biomass at structures, growth of YOY grayling at the structures was comparable to growth in control sections by late-July, with the exception of ramp1 (Fig. 6-6). Fish from ramp1 were almost 20% larger than the nearby control area (t-test; $P = 0.051$). Consistent with the general negative relationship between YOY size and distance downstream, YOY grayling from structures in the first 1500 m of

the artificial stream (groins and ramps) were larger than YOY from structures (vanes and v-weirs) in the lower end of the artificial stream (t-test; P = 0.01) (Fig. 6-6).

Artificial stream-Scale Assessment

Fish density and biomass

Fish densities differed among years (P = 0.003), between streams (P = 0.001), and between habitat types (P = 0.021), and there was a marginally significant interaction between year and stream (P = 0.056; Fig. 6-7a). These results were consistent among the general linear models for individual year pairs, however the interaction term (stream-by-year) was not significant for 1998 vs. 1999, indicating densities decreased similarly in both systems between those two years. Pairwise comparisons indicated that densities were higher in 2000 than in the two previous years, which themselves did not differ. Riffles generally supported higher fish densities than pools in both systems, and Polar-Vulture typically supported higher fish densities than the artificial stream. Stream effects generally increased over time and became significant in 1999-2000 (i.e., post-treatment).

Fish biomass was also affected by year (P = 0.010), stream (P = 0.001), and habitat type (P = 0.028), and there was a stronger interaction between year and stream (P = 0.010; Fig. 6-7b). Biomass was lower overall in 1999 than in 1998 or 2000, and was consistently higher in Polar-Vulture than in the artificial stream. Overall, the relative difference between the artificial stream and Polar-Vulture increased from 1998 to 2000 (i.e., post-treatment), although the increase was irregular in pool habitats.

YOY grayling growth

For the 1998-2001 study period, specific growth rate (SGR) differed among years (P = 0.001) and between the artificial stream and Polar-Vulture (P = 0.001). Although growth

was highest in all streams in 1998 and lowest in all streams in 2000, there was a significant year-by-stream interaction (P = 0.001; Fig. 6-8). The relative difference in growth between the artificial stream and Polar-Vulture was larger after structures were constructed (Fig. 6-8). The specific growth rates of grayling from Pigeon (1999-2001) and Polar-Panda (2000-2001) were consistently greater than the artificial stream fish (P = 0.001).

Discussion

Structure-Scale Assessment

Fish density

All structures were effective at attracting fish, as evidenced by the higher densities near structures in late-July, relative to neighboring control sites. Fish densities at ramp1 were particularly high, despite its upstream location, almost 2-fold higher than at other habitat structures and almost 4-fold higher than at many control sections of stream. It is thus likely that structures provided velocity refuge, visual isolation, and/or overhead cover, important components of habitat for stream fishes (Fausch 1993).

Young-of-the-year Arctic grayling experienced an ontogenetic shift in habitat use between the July and August sampling, reducing their concentration in the vicinity of the structures, particularly at vane and groin structures. However, ramp1 maintained a significantly higher density, relative to adjacent control sites, during the August sampling. Overall, fish density and biomass decreased 10 and 4-fold, respectively, but decreases were relatively greater at vanes and groins, falling below levels at the control sites. Observations from stream banks indicated that the two former structures provide quiet, shallow backwaters habitat for YOY grayling shortly after swim-up (early July),

but as they grew, YOY moved to deeper mid-channel habitats. In European grayling (*Thymallus thymallus L.*), this ontogenic shift occurs when fish exceed ca. 30 mm (Sempinski and Gaudin, 1995). Results from my study are generally consistent; Arctic grayling were 31 mm ± 4.5 SD and 46 mm ± 8.3 SD during the July and August samplings, respectively.

Fish growth

Despite the fact that higher densities of fish were attracted to structures, at least through July, growth of YOY Arctic grayling did not experience any density-dependent reduction (Keeley 2001), further suggesting that structures provided energetically favorable microhabitats. Ramp1 was particularly effective at increasing both the density of fish and the growth of YOY grayling, achieving levels of the latter that rivals growth in natural streams. An important reason for the success of this structure appeared related to its suitability for the production of black fly (*Simulium)* larvae. Unlike other structures, including ramp2, ramp1 decreased channel depth and forced the water to move swiftly over its incline, creating supercritical flow conditions that are favorable for black fly larvae attachment and capture of particulate organic matter (Hershey et al. 1995; Ciborowski et al. 1997). Indeed, relative to other sections of the artificial stream, ramp1 had extremely high densities of black flies (7 ind.$\cdot m^{-2}$ ± 3.6 SE vs. 2600 ind.$\cdot m^{-2}$, respectively; (N. Jones, unpubl. data).

In addition to the physical aspects of ramp1, its success is also likely related to the ecology of lake-outlet streams (see Haraldstad et al. 1987; Richardson and Mackay 1991). A steady supply of lake-derived energy (fine particulate and dissolved organic matter) often supports higher densities and biomass of filter-feeding benthic invertebrates

within the first 100-400 m of a lake in such streams (Carlsson et al. 1977). These filter-feeders, in turn, serve as prey for, and therefore attract, small fish (Gibson 2002). Although ramp1 is 1 km downstream from the lake, beyond the typical lake-outlet effect, it is the first location where critical flow velocities and suitable benthic habitat are provided, hence, it is likely the first location where large amounts organic matter are taken out of the water column by filter-feeders. Beyond ramp1, the next structures (v-weirs) were much farther downstream (ca. 1.5 km) from the Panda Lake outlet, well beyond a lake influence, but where adult fish concentrated to spawn. These downstream structures nevertheless supported initially higher biomass of YOY grayling relative to adjacent control sites due to the higher densities but comparable sizes of fish. Still, the much reduced food availability overall likely contributed to the smaller grayling at the downstream end of the artificial stream.

Stream-Scale Assessment

The density of fish in the artificial stream varied considerably among the 1998-2000 study years, in part related to variation in spawning stock size and also to climatic conditions. Spawning stock size increased consistently over time (1998: 103 adults, 1999: 185 adults, 2000: 411 adults, with 1:1 sex ratio), whereas the climatic conditions were most favorable in 1998 and least in 1999 (Chapter II). The same qualitative trend in density was noted in Polar-Vulture, which had consistently higher densities than the artificial stream, but density differences between the streams actually increased after structures were installed in the artificial stream (1999-2000). Fish biomass generally followed the trends observed in fish density. Relative to fish density and biomass in the

reference stream, there is little evidence to suggest that the habitat structures altered the productivity of the artificial stream at the whole-stream scale.

The specific growth rate (SGR) of YOY grayling also varied considerably among years. Although SGR in the artificial stream was highest in the year prior to structure construction (1998), this was also true for the reference stream (Polar-Vulture). During their first summer, growth of grayling is strongly affected by climate-related variables, including growing degree-days, discharge, and benthic invertebrate densities, and all were relatively favorable throughout the region in 1998 (Chapter II). Thus, any effect of the structures was overridden by the influence of these environmental factors. In fact, stream-scale differences in growth between the artificial stream and reference streams increased following the addition of the structures, similar to fish densities and biomass.

Structure Effectiveness: Scale of Measurement and the Role of Energy

My BACI-style examination of the effectiveness of habitat structures at enhancing productivity for fish, especially YOY Arctic grayling, revealed contrasting results at the two spatial scales examined. When comparing densities, biomass, and growth of fish at the instream structures, relative to nearby control sections, it was clear that the structures increased the availability of preferred fish habitat, especially early in the season, when YOY grayling were small. Observations of grayling in some sections of the artificial stream suggested that many YOY grayling opted for a "stayer" over a "mover" foraging strategy (Grant and Noakes 1987) once habitat structures were built. Undoubtedly some structures provided one or a combination of velocity refuge, visual isolation, and overhead cover, resulting in reduced energetic costs associated with foraging, maintaining position, predator vigilance or territoriality. I saw, however, no evidence of a

stream-scale enhancement of grayling in the artificial stream, either in an absolute sense or relative to reference streams. This suggests grayling were simply drawn from the nearly featureless control sections to structurally enhanced sections. As noted elsewhere, habitat enhancement can lead to a simple redistribution of animals without actually increasing total numbers, growth, or survival (Van Horne 1983; Reeves et al. 1991b; Gowan and Fausch 1996).

Although habitat structures likely provided favorable habitat for fish in the artificial stream, I suggest that a fundamental paucity of allochthonous and autochthonous organic matter was equally or more limiting to the production of YOY Arctic grayling (and their invertebrate prey) at the whole-stream scale than any structural deficiencies. Evidence for this stems from the hydraulic conditions created by ramp1 that facilitated the capture of allochthonous organic matter from the upstream lake by large numbers of black flies; in turn, this supported high densities of relatively large YOY. The other structures, however, were either unsuccessful (ramp2) or not designed for capturing imported energy, nor for facilitating autochthonous production.

Typically, the success of stream habitat modification or compensations projects is determined more by increasing the net productive capacity of a stream reach, rather than at an individual site, especially if the local increase is achieved simply at the expense of other sites. I suggest that a stream-scale benefit of structures in this artificial stream, and likely other habitat modification projects, may not be fully realized until more allochthonous and autochthonous organic matter is available to the benthic fauna and the fish. This suggestion emphasizes the importance of riparian vegetation and other functional biotic components of stream ecosystems to our restoration efforts (Sweeney

1992; Harrison and Harris 2002), and echoes the argument Sedell and Beschta (1991) to "bring back the bio in bioengineering".

For much of aquatic habitat compensation, the act of habitat restoration or enhancement is often seen as being more important and timely than rigorously examining causes of degradation, weighing alternative avenues of compensation, and assessing project effectiveness (Minns et al. 1996). Correspondingly, relatively few mitigation strategies and restoration techniques have been thoroughly evaluated (Reeves et al. 1991a). Ecological restoration is an emerging science and restoration programs are tests of our often limited ecological understanding; as such, our efforts will be fraught with mistakes (Bradshaw 1996). To avoid their repetition, a systematic approach to compensation is needed, grounded in the principles of the scientific method, including the use of appropriate references and spatial scales.

Literature Cited

Armstrong R.H. 1986. A review of Arctic grayling studies in Alaska, 1952 – 1982. Biological Papers of University of Alaska, Number 23: 3-17.

Beechie T. and Bolton S. 1999. An approach to restoring salmonid habitat-forming processes in Pacific Northwest watersheds. Fisheries 24: 6-15.

Bradshaw A.D. 1996. Underlying principles of restoration. Can. J. Fish. Aqua. Sci. 53(Suppl. 1): 3-9.

Carlsson M., Nilsson L.M., Svensson B.J., Ulfstrand S. and Wotton R. 1977. Lacustrine seston and other factors influencing the black flies (Diptera: Simuliidae) inhabiting lake outlets in Swedish Lapland. Oikos 29: 229-238.

Ciborowski J.J.H., Craig D.A. and Fry K.M. 1997. Dissolved organic matter as food for black fly larvae (Diptera: Simuliidae). J. N. Amer. Benthol. Soc. 16: 771-780.

Chapman M.G. 1999. Improving designs for measuring restoration in aquatic habitats. J. Aqua. Eco. Stress Recov. 6: 235-251.

Department of Fisheries and Oceans (DFO). 1986. The Department of Fisheries and Oceans policy for the management of fish habitat. Communications Directorate, Fisheries and Oceans, Ottawa, Ontario.

Fausch K.D. 1993. Experimental analysis of microhabitat selection by juvenile steelhead (Oncorhynchus mykiss) and coho salmon (O. kisutch) in a British Columbia stream. Can. J. Fish. Aqua. Sci. 50: 1198-1207.

Haraldstad O., Jonsson B., Sandlund O.T. and Schei T.A. 1987. Lake effect on stream living brown trout (*Salmo trutta*). Archiv für Hydrobiologia, 109, 39-48.

Harrison S.C. and Harris I.T. 2002. The effects of bankside management on chalk stream invertebrate communities. Freshwater Biology 47: 2233-2245.

Hershey A.E., Merritt R.W. and Miller M.C. 1995. Insect diversity, life history, and trophic dynamics in arctic streams, with particular emphasis on black flies (Diptera: Simuliidae). In: Arctic and Alpine Biodiversity. Ecological Studies Series Vol. 113 (Eds F.S. Chapin, III and C. Körner), pp. 283-294. Springer, Berlin Heidelberg, New York.

Hunter C.J. and Fernet D. 1990. Enhancement of artic grayling spawning in Hyalite Creek, Montana and the development of spawning habitat utilization curves. Proceedings Annual Conference Western Association Fish Wildlife Agencies, 70, 47.

Gibson R.J. 2002. The effects of fluvial processes and habitat heterogeneity on distribution, growth and densities of juvenile Atlantic salmon (Salmo salar L.), with consequences on abundance of the adult fish. Ecology of Freshwater Fish 11: 207-222.

Gowan C.G. and Fausch K.D. 1996. Long-term demographic responses of trout populations to habitat manipulation in six Colorado streams. Ecological Applications 6: 931-946.

Grant J.W.A. and Noakes D.L.G. 1987. Movers and stayers foraging tactics of young-of-the-year brook charr, Salvelinus fontinalis. J. Ani. Eco. 56: 1001-1014.

Keeley, E.R. 2001. Demographic responses to food and space competition by juvenile steelhead trout. Ecology 82: 1247-1259.

Lowe S. 1989. Fish habitat enhancement structures: typical structure designs. Alberta Environmental Protection, Water Resources Management Services, Technical Services and Monitoring Division, River Engineering Branch. Available: http://www3.gov.ab.ca/env/water/Reports/FishHabitat/index.html (November 2002).

Minns C.K. 1997. Quantifying "no net loss" of productivity of fish habitats. Can. J. Fish. Aqua. Sci. 54: 2463-2473.

Minns C.K., Kelso J.R.M. and Randall R.G. 1996. Detecting the response of fish to habitat alterations in freshwater systems. Can. J. Fish. Aqua. Sci. 53(Suppl. 1): 403-414.

Northcote T.G. 1995. Comparative biology and management of Arctic and European grayling (Salmonidae, Thymallus). Reviews in Fish Biology and Fisheries, 5: 141-194.

Reeves G.H., Everest F.H. and Sedell J.R. 1991a. Responses of anadromous salmonids to habitat modification: How do I measure them? In: Fisheries Bioengineering (Eds J. Colt and R. J. White), pp. 62-67. American Fisheries Society, Symposium 10, Bethesda, MD, USA.

Reeves G.H., Hall J.D., Roelofs T.D., Hickman T.L. and Baker C.O. 1991b. Rehabilitating and modifying stream habitats. In: Influences of Forest and Rangeland Management on Salmonid Fishes and Their Habitats (Ed W.R. Meehan), pp. 519-557. American Fisheries Society, Special Publication 19, Bethesda, MD, USA.

Richardson J.S. and Mackay R.J. 1991. Lake outlets and the distribution of filter feeders: an assessment of hypotheses. Oikos 62: 370-380.

Roni P., Beechie T.J., Bilby R.E., Leonetti F.E., Pollock M.M. and Press G.R. 2002. A review of stream restoration techniques and a hierarchical strategy for prioritizing restoration in Pacific Northwest Watersheds. N. Amer. J. Fish. Manag. 22:1-20.

Rosgen D.L. 1996. Applied River Morphology. Wildland Hydrology Books, Pagosa Springs, CO.

Schindler D.W. 2001. The cumulative effects of climate warming and other human stresses on Canadian freshwaters in the new millennium. Can. J. Fish. Aqua. Sci. 58: 18-29.

Sedell J.R. and Beschta R.L. 1991. Bringing back the "bio" in bioengineering. In: Fisheries Bioengineering (Eds J. Colt and R.J. White), pp. 160-175. American Fisheries Society, Symposium 10, Bethesda, MD, USA.

Sempeski P. and Gaudin P. 1995. Size-related changes in diel distribution of young grayling (*Thymallus thymallus*). Can. J. Fish. Aqua. Sci. 52: 1842-1848.

Stewart-Oaten A., Murdoch W.W. and Parker K.R. 1986. Environmental impact assessment: "pseudoreplication" in time? Ecology 67: 929-940.

Stirling J. 1979. The Sukunka story, an intimate look at Arctic grayling. Wildlife Review 9: 9-11.

Sweeny B.W. 1992. Streamside forests and the physical, chemical, and biological characteristics of Piedmont streams in Eastern North America. Water Science and Technology 26: 2653-2673.

Wesche T.A. 1985. Stream artificial stream modifications and reclamation structures to enhance fish habitat. In: The Restoration of Rivers and Streams: Theories and Experience (Ed J.A. Gore), pp. 103-163. Butterworth Publishers, Boston, MA.

White G.C., Anderson D.R., Burnham K.P., and Otis D.L. 1982. Capture-recapture and removal methods for sampling closed populations. Los Alamos National Laboratory LA-8787-NERP. 235 pp.

White R.J. (1996) Growth and development of North American stream habitat management for fish. Can. J. Fish. Aqua. Sci. 53(Suppl. 1): 342-363.

Van Horne B. 1983. Density as a misleading indicator of habitat quality. J. Wildl. Manag. 47: 893-901.

Zippin C. 1958. The removal method of population estimation. J. Wildl. Manag. 22: 82-86.

Table 6-1. Description of each structure type, the type of habitat type(s) it provides, the function of each structure with respect to the habitat needs of adult and YOY Arctic grayling, and the general influence on water velocities and depths (Wesche, 1985; Lowe, 1989; Rosgen, 1996).

Structure	Description	Habitat Structure	Function	Hydraulic effect
Ramp	Incline plane sloping downstream	Riffle	Spawning	Structure forces water shallow and fast.
V-weir	Large boulders forming a upstream pointing chevron	Pool and run	Nursery habitat and velocity refugia for migrating adults	Water flow is focused to the centre of the artificial stream. Depth created by scouring and turbulence created by weir boulders provide cover.
Vane	A series of five parallel finger-like projections perpendicular to shore consisting of large boulders	Riffle and shallow backwater	Nursery habitat and velocity refugia for migrating adults	Deflect the thalweg to opposite side of stream. Increase and decrease local water velocities. Promote point-bar formation via erosion of the opposite shore and deposition on proximate.
Groin	Single finger-like projections composed of large boulders angled ~45° downstream	Pool, run, and shallow backwater	Nursery and possibly spawning areas may be located off the tips of the structures	Deflect the thalweg to opposite side of stream. Increase local water velocities and scour potential.

Table 6-2. Mean length and area ± standard error of stream electrofished at sections of stream modified with structures and sections of stream used as controls in the artificial stream.

Structure	Vanes	V-weirs	Ramps	Groins	Controls
Length of stream (m)	19 (1.0)	4 (0.2)	11 (1.0)	6 (0.4)	62 (10.3)
Area (m^2)	37 (5.3)	18 (1.0)	44 (2.0)	9 (1.0)	282 (53.3)

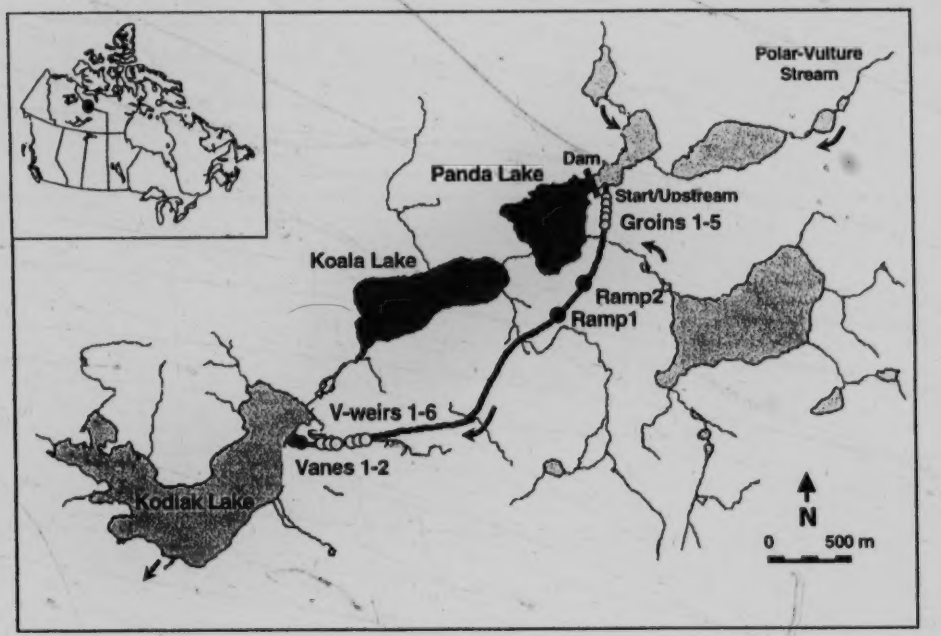

Figure 6-1. Map showing the location of the artificial stream in relation to lakes in the watershed. Koala Lake and the dark portion of Panda Lake were drained and developed as open-pit mines. Water flow is indicated by the arrows. The locations of fish habitat structures are indicated along the artificial stream. Insert: location of study area in the Northwest Territories, Canada.

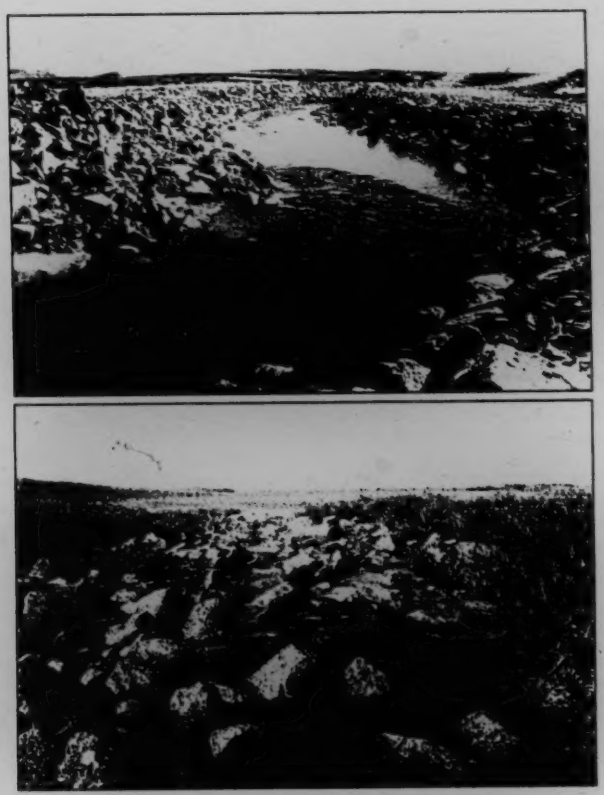

Figure 6-2. Pictures of the artificial stream (top) and a representative natural stream (bottom).

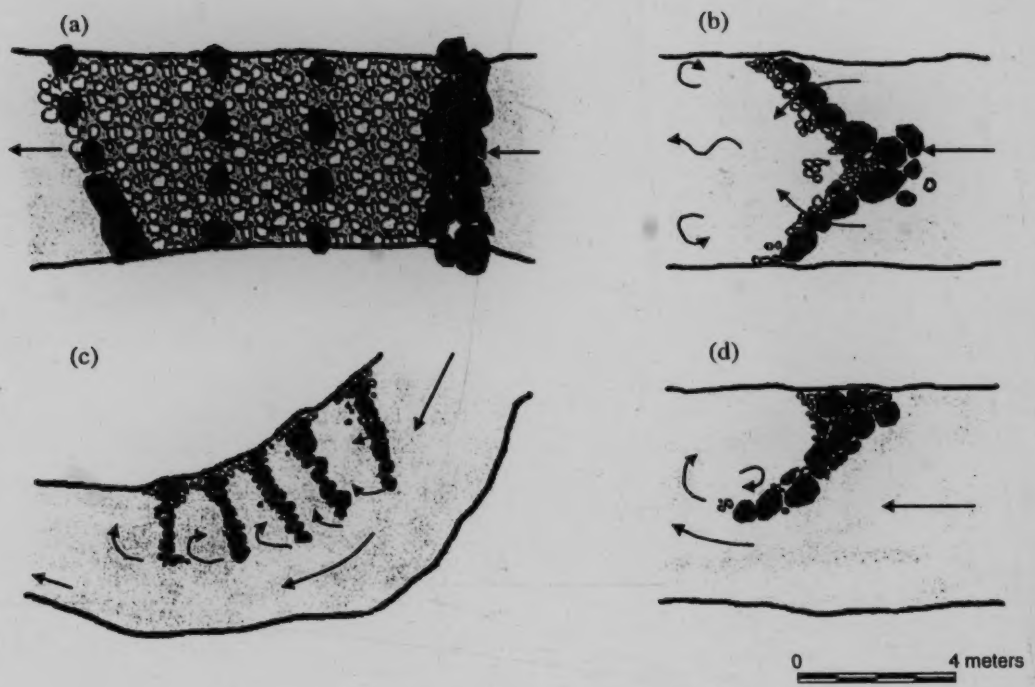

Figure 6-3. Planar views of each structure (a) ramp, (b) v-weir, (c) vanes, and (d) groin constructed in the artificial stream. Arrows indicate general direction of water movement.

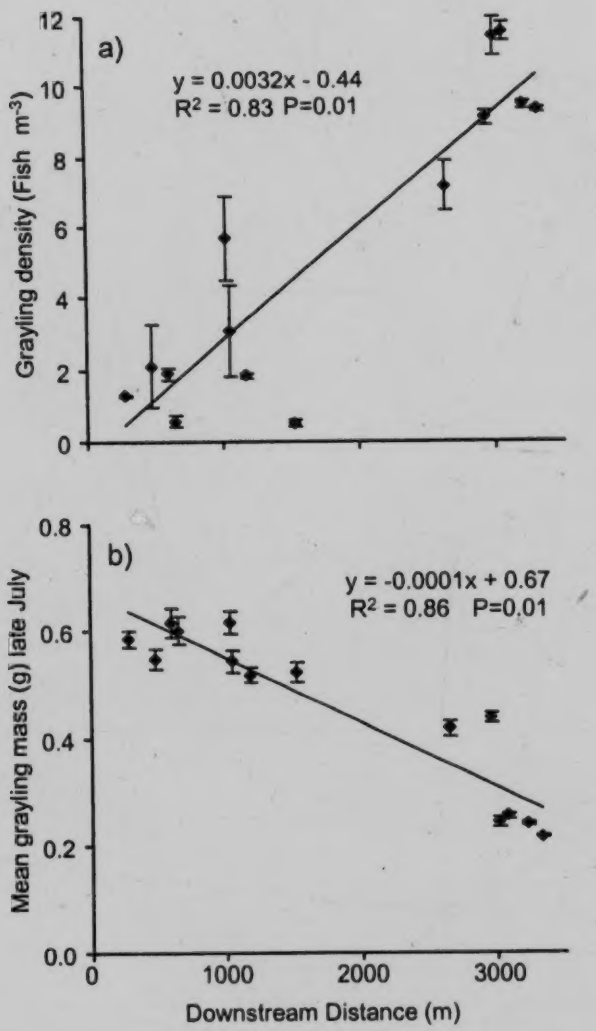

Figure 6-4. Mean density (a) and mass (b) ± SE of young-of-the-year Arctic grayling in relation to downstream distance from the lake outlet from control sections of the artificial stream in late July 2000. A 900 m stretch of the artificial stream, approximately midway between the source and mouth, is inaccessible to sampling.

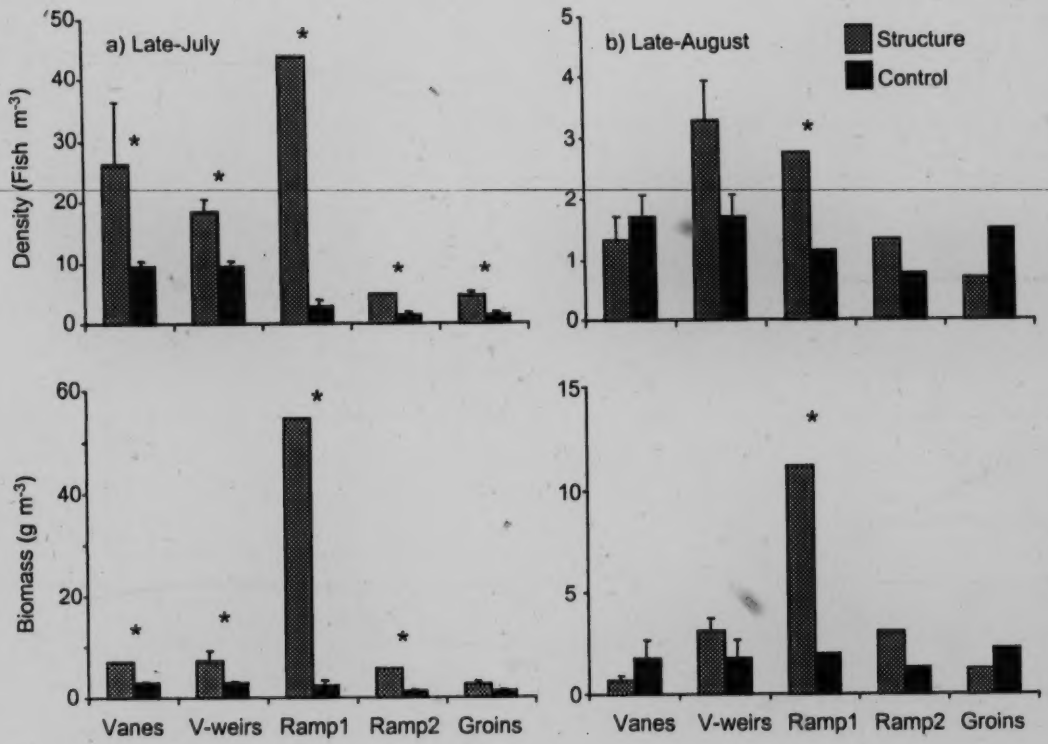

Figure 6-5. Mean ± SE density and biomass of fish at each structure and associated control sections of stream in late July (a) and August (b), 2000. Asterisks indicate significant differences (t-test with Bonferroni adjustment, $P < 0.05$).

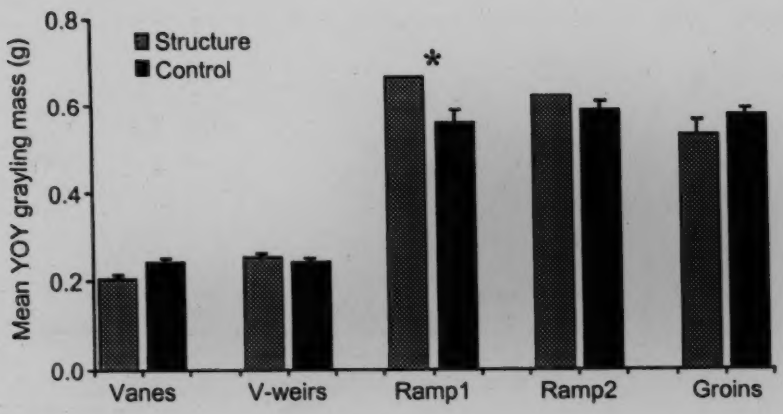

Figure 6-6. Mean ± SE mass of young-of-the-year Arctic grayling at each structure and associated control sections of stream in late July 2000. Average sample size is 147 fish per section of stream. Asterisks indicate significant differences (t-test, $P < 0.05$).

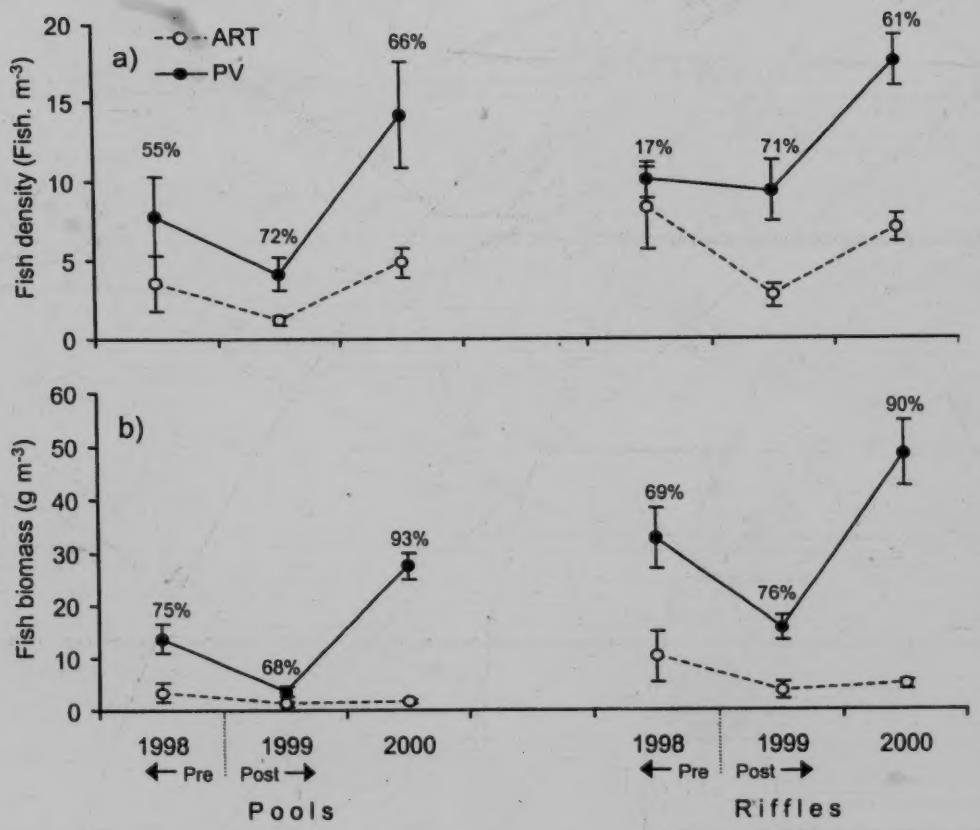

Figure 6-7. Mean ± SE density (a) and biomass (b) of fish in pool and riffle habitats in the artificial stream (ART) and Polar-Vulture stream (PV) in late-July, 1998 to 2000. Differences between the artificial stream and Polar-Vulture, expressed as percentages of the latter, are is listed above each bar. Dashed lines indicate pre- and post- construction periods for the structures.

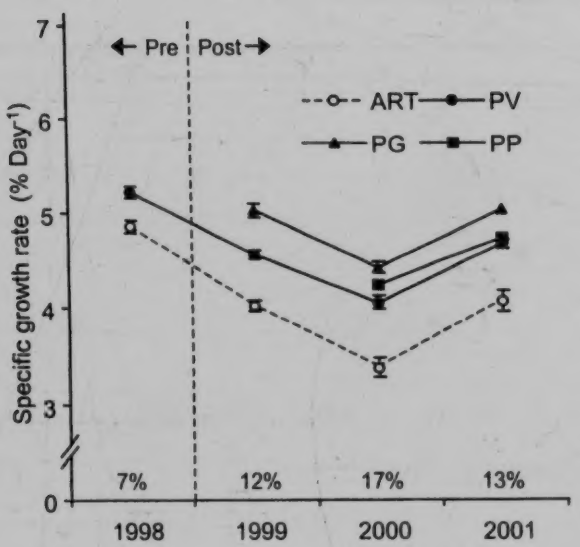

Figure 6-8. Growth rates ± SE of young-of-the-year Arctic grayling from swim-up to late-August for the artificial stream (ART) and three natural streams 1998-2001. Polar-Vulture (PV), Pigeon (PG), Polar-Panda (PP). Percentage difference between the artificial stream and natural streams are listed for each year along the abscissa. Dashed division lines indicate pre- and post-construction of the structures.

Chapter VII: General discussion

The supply and suitability of habitat ultimately limit fish populations (Minns 1997). Habitat loss and degradation caused by human development threaten the sustainability of fisheries resources. Under Canada's Fisheries Act, management strategies focus on preventing the harmful alteration, disruption, or destruction (HADD) of habitats that sustain fish productivity. Refinements of the Act led to the development of the "Policy for the Management of Fish Habitat" (DFO 1986), which has the principle of "no net loss of productive capacity of fish habitats" (NNL, Minns et al. 1996) to guide the management of fish habitat. Both HADD and NNL require, in theory, the ability to quantify the effects habitat change has on fisheries production. This, in turn, presumes that (i) the habitat needs of resident species are understood, (ii) the relationship between habitat and fish production is known, and (iii) there is a natural area or time prior to disturbance that can serve as a reference. In practice, this is often not the case. In particular, freshwater ecosystems of the Arctic and subarctic are among the least studied and most poorly understood in North America, as are their inhabitants, such as Arctic grayling. However, unlike other regions of the world, there are numerous streams in the Arctic that are largely pristine and provide excellent reference systems. The artificial stream and its fish habitat structures thus provide an tremendous opportunity to advance the study of fish habitat compensation and stream restoration ecology.

The assessment of the effectiveness of the artificial stream to compensate for lost habitat was based on a hierarchical framework of the specific functions that the artificial stream needed to provide in order achieve no net loss of productive capacity. Consistent

with NNL, the hierarchical framework of functions focused on the production of YOY Arctic grayling, that is, I asked can grayling successfully migrate through the channel, do the grayling spawn in the channel, do the eggs hatch in sufficient numbers, and do the young grayling grow to a sufficient size? Each of these functions is required for successful compensation for lost habitat and result in no net loss of productive capacity. Natural Barrenland streams provided reference standards and therefore enabled us to measure effectiveness of compensation efforts.

Because an ecological description of the streams lost during development, or Barrenland streams in general was not available, the use of natural, undisturbed streams was all the more important for establishing reference conditions to quantify gains and losses productive capacity of fish habitat. Given their remote arctic location, reference streams were assumed to fairly free of anthropogenic stress. Reference streams representing a range of physical, chemical, and biological characteristics observed in the Barrenlands region were effectively used to establish standards against which characteristics of the artificial stream could be compared (Chapter II).

In addition to a lack of understanding of ecology of Barrenland streams, a paucity of information also existed on the diet of Arctic grayling, particularly for young-of-the-year (YOY) (Armstrong 1986), information that was needed to assess the production capacity of the artificial stream. For example, it was critical to determine if an abundance of lake-derived prey, such as zooplankton (Schmidt and O'Brien 1982), provided adequate food to support grayling production. My quantification of YOY grayling diets (Chapter III) indicated that instream production of invertebrates, mainly Diptera, should largely determine the productive capacity of Barrenlands streams as fish habitat. Given the

necessary reference information on Barrenlands streams (Chapter II) and diet of YOY grayling (Chapter III), I could begin to make comparisons with the artificial stream (Chapter IV).

The artificial stream met or approached expectations for some of the functions of Barrenland streams listed above. Watershed connectivity was at least partially restored and this allowed adult grayling to migrate throughout the drainage basin, i.e., the artificial stream restored landscape-scale habitat use. Because Barrenlands grayling, with their adfluvial life history, migrate among the chains of lakes and streams in the drainage basin, its fragmentation would have meant the loss of habitat availability at this scale, which could have had significant population-level consequences (Kentaro and Shoichiro 2002). As such, restoring watershed connectivity was paramount in the development of the artificial stream. Although passage throughout the artificial stream was achieved for adult grayling and lake trout, slimy sculpin and burbot appeared unable to ascend one of the culverts, suggesting that their populations in the watershed have become fragmented. Within the artificial stream, fish passage was needed so that grayling could move to and select among available spawning areas. Although a quantitative estimate of spawning success was not determined, I noted qualitatively that YOY grayling were produced in large numbers, particularly in the lower end of the stream where the majority of spawning occurred.

Despite these successes, the growth and production of YOY grayling strongly suggested that the quality of nursery habitat in the artificial stream is deficient in some manner. In Chapter IV, I examined three possible explanations for the differences seen in the growth of YOY grayling, food production, water temperature and physical habitat.

Through bioenergetic simulations it became clear that the cooler water temperatures in the artificial stream had limited influence on growth, whereas, low amounts of autochthonous primary production and low inputs of allochthonous organic matter limited the productivity of benthic invertebrates in the artificial stream and ultimately limited the growth and production of young-of-the-year grayling, relative to reference streams. The magnitude of the effect that physical habitat had on productivity was less clear and difficult to objectively assess within my bioenergetic framework.

In chapter V, I used an alternative quantitative method, namely resource selection functions (Boyce and McDonald 1999), to examine not only what habitat characteristics influence the locations chosen by two size-classes of YOY grayling in natural streams, but also to assess the quality of habitat available for grayling in the artificial stream. Habitat selected by small YOY grayling was best described by shallow and slow-moving water found near stream banks and pocket water in riffle habitats common in natural Barrenland streams. In contrast, large YOY grayling selected deeper and faster water in association with riffle habitat at mid-stream locations with a diversity of cover types. Although these latter quality habitats were common in Polar-Vulture, a nearby reference stream, they were deficient in the artificial stream. As a result, the larger YOY were forced to use habitat that would not be used in the natural streams. This quantitative assessment of physical habitat agrees with general observations of habitat quality, and more importantly, with the poor growth and lower density and biomass of YOY observed in the artificial stream relative to the natural streams (Chapter IV). Results of Chapter V thus suggested that poor physical habitat played an important role, by failing to provide

adequate habitat, including such features as velocity refugia, visual isolation, and overhead cover (Fausch 1993).

To improve stream habitat for fish, managers frequently focus on physical characteristics and install instream structures that can provide the aforementioned features. In this tradition, managers of the artificial stream added examples of five different types of structures to the stream at the end of the first year. Although the spatial distribution of these structures was not ideal, the timing of their installation and the availability of reference streams allowed for a BACI design (before, after, control, impact) to assess the effectiveness of the structures (Chapter VI). Findings of Chapter VI were consistent with the hypothesis that the quality of physical habitat was poor in the "as built" artificial stream, in that the addition of physical habitat structures attracted higher densities of YOY grayling than did nearby non-enhanced sections. Despite the fact that higher densities of fish were attracted to structures, the growth of YOY Arctic grayling did not experience any density-dependent reduction, further suggesting that structures provided energetically favorable microhabitats. Relative to reference streams and pre-structure conditions, however, the addition of these physical structures did not increase the density, biomass, or growth rates of YOY grayling in the artificial stream as a whole. At this larger scale, weather conditions and a lake-outlet effect strongly affected the production of grayling. It is likely that a stream-scale benefit of structures in this artificial stream will not be fully realized until more allochthonous and autochthonous organic matter is available to the benthic fauna and fish.

The rocky ramp was the only structure that produced grayling rivalling the sizes of YOY in natural streams. The success of this structure was probably related to its physical

characteristics, which were suitable to allow *Simulium* larvae to capture the steady supply of lake-derived energy (fine particulate and dissolved organic matter) often associated with lake-outlet streams (see Carlsson et al. 1977; Haraldstad et al. 1987; Richardson and Mackay 1991; Hershey et al. 1995; Ciborowski et al. 1997). Thus, although the physical characteristics of this structure were important in the enhanced production of food for grayling, it was the lake-derived supply of organic energy that was ultimately important. How much energy the upstream lake can provide to instream production for the artificial stream is unknown but it is likely limited (Richardson and Mackay 1991).

My assessment of the productive capacity of the artificial stream should allow managers to make defensible decisions (*sensu* Minns et al. 1995) and guide the subsequent work that will be required for continued compensation. The objectives of future studies will need to consider a number of important questions, such as (i) what can be done to improve the growth of grayling while continuing to learn about fish habitat compensation in the Arctic, (ii) at what point will grayling have reached acceptable growth, (iii) how long should compensation take, and (iv) because the artificial stream is a completely new ecosystem and ecological succession in the Arctic is slow, how can the successional process be sped up? These questions are challenging, but the characteristics of this ecosystem and the information that my studies have provided offer tremendous opportunity to advance the study of fish habitat compensation and stream restoration ecology in the Arctic and elsewhere.

Actions at this point should clearly focus on increasing this size of YOY in the artificial stream to that observed in natural streams. Although the current paucity of autochthonous and riparian-based organic matter in the artificial stream is ultimately

limiting growth and production of YOY grayling, physical habitat also appears to play a role. However, instead of haphazardly modifying the artificial stream in an effort to improve its productivity capacity, a practice that seems too common in restoration, the modifications to the artificial stream should be done in a experimental manner, with replicates and controls that would enable cause and effects of actions to be learned. Perhaps more ramp structures could be added to the artificial stream at a gradient of distances from the upstream lake to better understand the amount and fate of imported energy and ecology of lake-outlet streams. Next, riparian vegetation could be added in quantities similar to those observed in Barrenland streams, followed by treatments of aquatic vegetation and organic matter such that the effects of each treatment could be assessed. In doing so, the relative influences of physical habitat and organic matter on the growth of grayling may become clear. This experimental management approach would create many opportunities for continued learning about the relationships between fish and fish habitat so desperately needed in northern Canada. In essence, every fish habitat compensation program should be structured as an experiment in such a way to test hypotheses about aquatic ecosystems. This approach is similar to that envisioned by Harper (1987), who saw the heuristic value of ecological restoration. Restoration is more than a technique orientated, empirically driven, applied science, it is a way of raising basic questions and testing fundamental hypotheses about the communities and ecosystems being restored. Taken further, ecological restoration may represent the "acid test" of our ecological understanding, determining if we can take ecosystems apart and put them together and make them work (Bradshaw 1987). The current lack of knowledge about which mitigation and compensation methods are successful and where they are

appropriate provides impetus for using an experimental approach when managing fish habitat. Compensation agreements should explicitly acknowledge the importance of experimentation and adaptive management.

At what point will grayling have reached acceptable growth in the artificial stream? More specifically, when will they reach a size that managers will consider as adequate to survive to adulthood and perpetuate the population? Should it be when the growth lies within the range of natural variability observed in Barrenland streams, or perhaps when the growth is no different than the average growth observed in several Barrenland streams? And how will this be assessed statistically? These questions have important implications for the ultimate success of the compensation program. The probability of an individual fish surviving a period of low food availability, such as the long arctic winter, is largely size-dependent based on their energy reserves and the rate at which they are used metabolically (Post and Evans 1989; Post et al. 1999).

As of 2001, YOY grayling in the artificial stream reached an end-of-summer mass approximately half that observed in natural streams. It is therefore reasonable to suggest that they will experience reduced survival during their first winter. In turn, recruitment into the breeding population may be impaired and thus the long-term sustainability of the population questionable. To accurately predict the size and numbers of YOY needed to survive to adulthood in each generation to perpetuate the population, rather than use the sizes achieved by fish in the natural streams, would be extremely challenging, particularly in the absence of empirical data. Many Arctic populations of fish have long generation times (i.e., mature late), thus, assessing the adequacy of compensation by monitoring numbers of returning adult fish may not be completed until after it is too late

for adjustments in the adaptive management process. Perhaps more challenging would be the direct assessment of the adult population in the complex system of chain-lakes common in the Barrenlands.

How long should compensation take in the Arctic? The effects of disturbance in the Arctic can be long lasting, sometimes irreversible (Reynolds and Tenhunen 1996). O'Neill (1976) modeled the recovery of various ecological communities ranging in productivity to a standard perturbation and found that the flux of energy through a system of three components (active plant tissue, heterotrophs, and inactive organic matter) has important influences on ecosystem resilience. Pond ecosystems recovered remarkably fast because they have a relatively low standing crop and high rates of biomass turnover, while tundra systems were the slowest to recover. Without intervention, the artificial stream ecosystem could take hundreds of years to develop conditions with the structure and function resembling that of natural streams. Should activities that speed restoration be included in the compensation program? Perhaps habitat alteration in the north should be seen as more damaging and thus require more compensation effort, or less initial impact should be permitted than in aquatic ecosystems in the more southerly, productive, and resilient locations?

What is a successful habitat compensation? The Policy for the Management of Fish Habitat (DFO 1986) views success as being when productive capacity, the maximum natural capability of habitats to produce healthy fish, safe for human consumption, or to support or produce aquatic organisms upon which fish depend, is restored. Many argue that taking such an ichthyo-centric view is acceptable because fish are symbolic of the health of ecosystems and our ability to manage our resources (e.g., Karr 1981, Fausch et

al. 1990; Whitfield and Elliott 2002). Fish are relatively long-lived, can require distinct habitats during various life history stages, and are generally sensitive to environmental stressors and pollutants and, as such, they integrate the effects of their environment (Schiemer 2000). Many fish occupy high trophic positions, and as such, rely on production in lower trophic levels, which is explicitly acknowledged in DFO's (1986) definition of productive capacity. However, some may criticize this ichthyo-centred view. Should the goal of habitat management and compensation be focused on fish production? Some may demand that policy move beyond productive capacity (Jones et al. 1996), to include aspects of ecosystem integrity and health (Rapport 1992; Costanza and Magaue 1999). In this sense, compensation is obtained when selected indicators of ecological structure (e.g., species richness and composition, trophic organization, and habitat status), function (e.g., primary production, energy and material flows) remain within limits that are agreed as likely to avoid a significant risk of progressive or irreversible change or decline.

Regardless of the assessment approach taken, habitat compensation projects need to be formally examined, as in the present study, and not just merely constructed. Questions must be asked: did the compensation work? What did we do right? What was done wrong? And, why? These assessments must be grounded in the principles of the scientific method, including the use of appropriate reference sites, and a strong commitment must be made to publish results in peer-reviewed journals (Bradshaw 1996; Minns et al. 1996), for only then we can begin to learn from our collective experiences and improve decision-making for tomorrow.

Literature Cited

Armstrong, R.H. 1986. A review of Arctic grayling studies in Alaska, 1952-1982. Biological Papers of the University of Alaska. No. 23.

Boyce, M.S., and McDonald, L.L. 1999. Relating populations to habitats using resource selection functions. Trends in Ecology and Evolution 14: 268-272.

Bradshaw, A. D. 1987. Restoration: an acid test for ecology. In: W. R. I. Jordan, M. E. Gilpin and J. D. Aber (ed), Restoration Ecology: A Synthetic Approach to Ecological Research. Cambridge University Press, Cambridge, pp. 23-29.

Department of Fisheries and Oceans (DFO). 1986. The Department of Fisheries and Oceans policy for the management of fish habitat. Communications Directorate, Fisheries and Oceans, Ottawa, Ontario.

Cairns, J. J. 1987. Disturbed ecosystems as opportunities for research in restoration ecology. In: W. R. I. Jordan, M. E. Gilpin and J. D. Aber (ed), Restoration Ecology: A Synthetic Approach to Ecological Research. Cambridge University Press, Cambridge, pp. 307-320.

Carlsson M., Nilsson L.M., Svensson B.J., Ulfstrand S. and Wotton R. 1977. Lacustrine seston and other factors influencing the black flies (Diptera: Simuliidae) inhabiting lake outlets in Swedish Lapland. Oikos 29: 229-238.

Ciborowski J.J.H., Craig D.A. and Fry K.M. (1997) Dissolved organic matter as food for black fly larvae (Diptera: Simuliidae). J. N. Amer. Bentholo. Soc. 16: 771-780.

Costanza R and Mageau M. 1999. What is a healthy ecosystem? Aquatic Ecol 33:105-15

Fausch, K. D., J. Lyons, J. R. Karr, and P. L. Angermeier. 1990. Fish communities as indicators of environ-mental degradation. Amer. Fish. Soc. Symp. 8:123-144.

Haraldstad O., Jonsson B., Sandlund O.T. and Schei T.A. 1987. Lake effect on stream living brown trout (Salmo trutta). Archiv für Hydrobiologia 109: 39-48.

Harper, J. L. 1987. The heuristic value of ecological restoration. In W. R. I. Jordan, M. E. Gilpin and J. D. Aber (ed), Restoration Ecology: A Synthetic Approach to Ecological Research. Cambridge University Press, Cambridge, 35-45.

Hershey A.E., Merritt R.W. and Miller M.C. 1995. Insect diversity, life history, and trophic dynamics in arctic streams, with particular emphasis on black flies (Diptera: Simuliidae). In: Arctic and Alpine Biodiversity. Ecological Studies Series Vol. 113 (Eds F.S. Chapin, III and C. Körner), pp. 283-294. Springer, New York.

Jones, M.L., R.G. Randall, D. Hayes, W. Dunlop, J. Imhof, G. Lacroix and N.J.R. Ward. 1996. Assessing the ecological effects of habitat change: moving beyond productive capacity. Can. J. Fish. Aquat. Sci. 53(Suppl. 1): 446-457.

Karr, J.R. 1981. Assessment of biotic integrity using fish communities. Fisheries 6:21-27.

Karr JR. 1991. Biological integrity: a long neglected aspect of water resource management. Ecol Applications 1: 66-84

Kentaro, M. and Shoichiro, Y. 2002. Effects of habitat fragmentation by damming on the persistence of stream-dwelling charr populations. Conserv. Bio. 16: 1318-1323.

Minns, C.K., Meisner, J.D., Moore, J.E., Greig, L.A., and Randall, R.G. 1995. Defensible methods for pre- and post-development assessment of fish habitat in the Great Lakes. A prototype methodology for headlands and offshore structures. Can. MS Rep. Fish. Aquat. Sci. 2328.

Minns, C.K., Kelso, J.R.M., and Randall, R.G. 1996. Detecting the response of fish to habitat alterations in freshwater systems. Can. J. Fish. Aquat. Sci. 53(Suppl. 1): 403-414.

O'Neill, R.V. 1976. Ecosystem persistence and heterotrophic regulation. Ecology 57: 1244-1253.

Post, J.R., and Evans, D.O. 1989. Size-dependent overwinter mortality of young-of-the-year yellow perch (*Perca flavenscens*): laboratory, in situ enclosure, and field experiments. Can. J. Fish. Aquat. Sci. 46: 1958-1968

Post, J.R., Parkinson, E.A., and Johnston, N.T. 1999. Density-dependent processes in structured fish populations: interaction strengths in whole lake experiments. Ecol. Mono. 69: 155-175.

Rapport, D.J. 1992. Evaluating ecosystem health. J. Aqua. Eco. Health. 1: 15-24

Reynolds, J.F. and Tenhunen, J.D. (eds.), 1996: Landscape Function and Disturbance in Arctic Tundra. Springer-Verlag, Ecological Studies Series Volume 120. New York: Springer-Verlag. 437 pp.

Richardson J.S. and Mackay R.J. 1991. Lake outlets and the distribution of filter feeders: an assessment of hypotheses. Oikos 62: 370-380.

Schmidt, D., and W.J. O'Brien. 1982. Planktivorous feeding ecology of arctic grayling (*Thymallus arcticus*). Can. J. Fish Aquat. Sci. 39:475-482

Schiemer, F. 2000. Fish as indicators for the assessment of the ecological integrity of large rivers. Hydrobiologia 422/423: 271-278.

Whitfield, A.K. and M. Elliott. 2002. Fishes as indicators of environmental and ecological changes within estuaries: a review of progress and some suggestions for the future. J. Fish Bio. 61(Suppl.): 229-250.